

Ordovician trilobites from the Tourmakeady Limestone, western Ireland

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SYNOPSIS. Trilobites of the Tourmakeady Limestone, County Mayo, western Ireland, comprise 23 species and genera. This fauna is an early example of the Illaenid-Cheirurid biofacies, being dominated by a few species of the families Illaenidae, Cheiruridae and Celmididae. It is basal Whiterockian (upper Arenig) in age. Several of the trilobites are early representatives of clades which achieved subsequent prominence. All but one of the species are represented by silicified material, and many are supplemented by crackout specimens. Four trilobite species have been previously named: *Kawina divergens*, *Niobe ornata*, *Oopsites hibernicus* and *Illaeus weaveri*, and are revised herein. One genus, *Mayopyge* (type species *M. zapata* sp. nov.), is new, as are the species *Phaseolops ceryx*, *Protostygina coronula*, *Glaphurus crinitus*, *Dimeropyge? ericina*, *Celmus michaelmus*, *Agerina palabunda*, *Proscharyia platylimbata* and *Ceratocephalina ramskoeldi*. The remaining species are described in open nomenclature.

INTRODUCTION

The occurrence of trilobites in the upper Arenig Tourmakeady Limestone was recognized at the time Gardiner & Reynolds (1909, 1910) undertook the initial geological description of the Ordovician inliers of the Tourmakeady and Glensaul districts. Reed illustrated a few sclerites (in Gardiner & Reynolds 1909), and named two species. He later (1945) proposed a further two species, based on the illustrations of the 1909 work, but the scope and quality of the Tourmakeady faunas were not fully appreciated until the discovery by Williams in the 1960s that much of the material was silicified. Williams & Curry (1985) have subsequently described the rich brachiopod faunas of the unit, but the trilobites have only seen limited treatment. The trilobites described here were derived from the residues sorted by Williams & Curry (1985). Fortey (1975a, 1980) has illustrated some specimens for comparison with conspecific or closely related taxa from Spitsbergen. Fortey & Owens (1975) figured some sclerites to illustrate concepts within their new Proetida, and Fortey (1975b: 345) gave a preliminary sclerite count in a discussion of Early Ordovician trilobite communities.

The aim of the present work is the systematic description of the entire Tourmakeady trilobite fauna, based on all available material. The fauna is of interest particularly because of its stratigraphic position near the base of the Middle Ordovician. This was a time of significant phylogenetic turnover of trilobites, and the Tourmakeady assemblage contains several forms important to an understanding of this change.

AGE, PRESERVATION, AND COMPOSITION OF THE FAUNA

The Tourmakeady Limestone occurs as blocks within bedded tuffs and grits of the 'Shangort and Tourmakeady Beds' of Gardiner & Reynolds (1909, 1910). This was mapped by Williams & Curry (1985: fig. 1) as part of the Glensaul Group. Evidence of the age of the Tourmakeady Limestone is derived from graptolite collections reported from beds above and below the limestone blocks, and from the trilobites and brachiopods themselves.

The trilobites from the white crackout limestones are invariably

undistorted. Those from the blocks yielding silicified trilobites often show a modest degree of distortion (as do most of the brachiopods figured by Williams & Curry (1985)). At least one silicified sample yielding the type material of *Glaphurus crinitus* is without distortion. We do not understand the reasons for these differences. Possibly they are related to silicification having occurred near faults. Whatever the cause, there appears to be no important difference in faunal composition between crackout and silicified collections. Relative abundances of particular taxa vary significantly between the crackout and silicified samples, but this is certainly due to the ease with which smoother, larger, and less convex specimens crack out.

Graptolites were reported by Dewey *et al.* (1970) from several localities on the western margin of Lough Mask. Three collections indicate that the underlying Mount Partry Group belongs to what they termed the '*Didymograptus protobifidus* Zone of North America'. Williams & Stevens (1988) doubted that the '*protobifidus* Zone' could be reliably distinguished from the North American *Didymograptus bifidus* Zone, which had been claimed to overlie it. This interval (*bifidus* + *protobifidus*) equates with the Chewtonian Stage of the Australian graptolitic standard, and with the mid-part of the Arenig Series of the Anglo-Welsh succession. Graptolitic rocks of the *D. bifidus* Zone are associated with the shelly Zone J faunas in the western USA (Braithwaite 1976), and hence with the upper part of the Ibexian Series of the North American stratigraphic standard in Utah (Ross *et al.*, 1993).

Within the Glensaul Group Dewey *et al.* (1970) listed a graptolite (fauna 4 on their fig. 2) from below the Tourmakeady Limestone which they state is 'intermediate between *Isograptus caduceus* var *victoriae* Harris and *I. caduceus* var *lunatus* Harris'. These varieties are usually regarded as subspecies of *I. victoriae* in current usage (e.g. Cooper & Lindholm 1991) and their intergradation occurs within the Castlemainian Stage at the junction of Ca1 and Ca2. A graptolite fauna from above the Tourmakeady limestone (Fauna 7 of Dewey *et al.* 1970: 29–30) yielded biserial graptoloids including *Undulograptus austrodentatus*; also listed is a didymograptid described as *Didymograptus* sp. 2, which seems to belong to the genus *Xiphograptus* Cooper & Fortey, 1982. The combination of *austrodentatus* group biserial graptoloids with *Xiphograptus* embraces a short interval at the top of the Arenig series (Mitchell & Maletz 1995), and at the base of the Darriwillian Stage of the Australian scheme.

Thus the time of Tourmakeady Limestone deposition is bracketed by graptolite faunas, which indicate it must be upper Castlemainian to Yapeenian, and late Arenig in terms of the Anglo-Welsh standard. This is consistent with the trilobite evidence cited below.

Williams & Curry (1985) stated that the Tourmakeady brachiopod fauna was 'equivalent to Zone K' of the North American shelly standard zonation. Zone K is a thin brachiopod coquina composed entirely of *Hesperonomiella minor* Cooper which is exposed in several sections in Utah and Nevada. Ross *et al.* (1993) no longer recognised it biostratigraphically, but incorporated it within the terminal Ibexian. Nonetheless, its position above Zone J does seem to be consistent with the occurrence of the Tourmakeady Limestone above Zone J equivalents in western Ireland.

Trilobite faunas described below are dominated numerically by Illaenidae, Cheiruridae and celmids. As Fortey (1975b) originally pointed out, it is an illaenid-cheirurid biofacies fauna, associated with a limestone mound. The biogeographic affinities of the fauna are overwhelmingly Laurentian. Comparison is made first with two faunas previously known from Laurentia: the white limestone boulder at Lower Head, western Newfoundland (Whittington 1963) and the Meiklejohn bioherm in the western USA (Ross 1972). The latter lies above the Ninemile Formation which yielded a Zone J trilobite and graptolite fauna; the Lower Head Boulder (James & Stevens 1986: fig. 40) lies above a sparse Cal graptolite fauna. Hence, both occupy stratigraphically comparable positions to the Tourmakeady Limestone. The Lower Head fauna is most similar. A species of *Geragnostus* is in common, while close comparisons are made with species of *Nileus*, *Illaeus*, *Glaphurus*, *Kawina*, *Isocolus*, *Celmus*, and *Phaseolops*. The first four genera named are present also in the Meiklejohn Peak, known from sparser material. The fact that the species are almost all different in points of fine detail allows for some difference in age between the Tourmakeady and Cow Head, but the difference cannot be great. Both these previously described faunas have been regarded as equivalent to Zone L (*Psephosthenaspis* Zone) of the Utah/Nevada stratigraphic standard, lying at the base of the Middle Ordovician (i.e., base of the Whiterockian) in North American terms. In its type section, this is developed in bathyrid biofacies (Fortey & Droser 1996) and hence has a different suite of taxa from the Tourmakeady Limestone. Note that younger (Zone M) Whiterockian faunas, similar to those of the Table Head Formation, western Newfoundland, are known in the Tourmakeady area from the base of the younger Glendavock Formation (Pudsey 1984). There are a few similarities at species level between the Tourmakeady and faunas of generally deeper-water biofacies described from the Valhalla Formation, Spitsbergen. The pelagic trilobites *Opiputer inconnivus* Fortey, 1974 and *Oopsites hibernicus* (Reed in Gardiner & Reynolds, 1909) are both known from the Olenidsletta Member, where their ranges extend to just below the first occurrence of *Isograptus victoriae victoriae* (Fortey 1980; Cooper & Fortey 1982). Fortey (1975a: 31) suggested that *Niobe occulta* was virtually indistinguishable from the extremely fragmentary species from the Tourmakeady Limestone described by Reed (1945) as *Niobe ornata*. The species has a short range through the upper mid-part of the Olenidsletta Member, where it occurs immediately below beds with *Isograptus victoriae*, and immediately above the interval carrying *Oopsites hibernicus* and *Opiputer inconnivus*, which was equated by Fortey (1980) with Zone J. Hence the Tourmakeady fauna is rather tightly constrained by species comparisons as lying within a short interval of the late Arenig between latest Chewtonian and early Castlemainian in graptolite terms.

In the platform sections of Utah and Nevada there is a sequence boundary just above the 'Zone K' brachiopod coquina and below the first trilobite fauna of the *Psephosthenaspis* (L) Zone. If this regres-

sive event were global, it is possible that this is the time at which illaenid-cheirurid 'mounds' developed in the volcanic setting of the South Mayo trough, since lowstands on the platform equate with enhanced deposition of fringing carbonates on offshore island sites. The Tourmakeady fauna might 'fit in' to the hiatus at the base of the North American Middle Ordovician. In the Meiklejohn 'reef' there is a 2 m interval of birdseye limestone without macrofossils above Zone J and below the bioherm itself, which occupies a comparable stratigraphical position.

Numbers of trilobite individuals for each species recovered from the entire silicified collection are given in Table 1.

Table 1 Number of cranidia (*cr.*), pygidia (*pyg.*), and individuals (*ind.*) for all species recovered from silicified residues of the Tourmakeady Limestone, together with relative proportion of total number (% *tot*) of individuals (894) recovered. The single known pygidium of *Niobe ornata* (Reed, 1945), is a calcareous crackout specimen and is listed for completeness; no other species are known exclusively from non-silicified material.

	<i>cr.</i>	<i>pyg.</i>	<i>ind.</i>	% <i>tot</i>
<i>Celmus michaelmus</i>	276	4	276	30.9
<i>Mayopyge zapata</i>	265	50	265	29.6
<i>Illaeus weaveri</i>	109	99	109	12.2
<i>Geragnostus clusus</i>	31	14	31	3.5
<i>Oopsites hibernicus</i>	28	7	28	3.1
<i>Dimeropyge? ericina</i>	27	0	27	3.0
<i>Proscharyia platylimbata</i>	25	5	25	2.8
<i>Glaphurus crinitus</i>	23	0	23	2.6
<i>Agerina palabunda</i>	22	0	22	2.5
<i>Phaseolops ceryx</i>	20	6	20	2.2
<i>Opiputer aff. O. inconnivus</i>	12	0	12	1.3
<i>Nileus</i> sp.	7	12	12	1.3
<i>Benthmaspis</i> aff. <i>B. diminutiva</i>	5	10	10	1.1
Catillicephalid gen. nov.	7	0	7	0.8
<i>Isocolus</i> sp. nov. A	6	2	6	0.7
<i>Kawina divergens</i>	6	1	6	0.7
<i>Ceraurinaella</i> sp.	5	4	5	0.6
<i>Ceratocephalina ramskoeldi</i>	4	1	4	0.4
<i>Protostygina coronula</i>	2	2	2	0.2
<i>Ampyx</i> cf. <i>toxotis</i>	1	1	1	0.1
<i>Dividuagnostus</i> sp. indet.	1	0	1	0.1
<i>Cybelina</i> sp.	1	0	1	0.1
<i>Niobe ornata</i>	0	1	1	0.1

ORDOVICIAN INSULAR FAUNAS, BIOGEOGRAPHY AND TAXONOMIC NOVELTY

Neuman (1984) has discussed how Ordovician brachiopod faunas from ancient island sites include a mixture of endemic genera, often with alleged first occurrences of 'ancestors' of forms known from younger rocks in platform successions. The implication is that such islands may have been sources of speciation leading to subsequent clades. The Ordovician South Mayo trough included a number of volcanic centres, possibly as part of a marginal basin resembling the Gulf of California (Ryan & Archer 1978). The fact that Williams & Curry (1985) reported some twelve new genera from the Tourmakeady brachiopods invites the question whether the trilobites show a similar 'insular' trend.

There is one endemic catillicephalid genus which we are unable to name formally. The fauna includes what may be the oldest known protoidean, *Phaseolops*, a group which became progressively more important through the Ordovician and later. The other typical repre-

sentatives of the illaenid-cheirurid biofacies (*Illaeus*, *Glaphurus*, *Ischyrotoma*, *Kawina*, etc.) are represented quite widely in contemporary deposits (e.g., Ingham *et al.*, 1986). The pelagic trilobites *Opiputea* and *Opsites* are globally distributed at low palaeolatitudes (Cocks & Fortey 1990: fig. 2).

The recognition of phylogenetic affinities of some of these taxa with much older forms, for example, the glaphurids with the Cambrian raymondinids and the isocolids with the catiliccephalids, serves to remove any notion of novelty from these faunal elements. This leaves *Phaseolops* as the sole example of a precocious genus of higher taxa, and we can match such single examples in several other faunas at the base of the Middle Ordovician, which was an important watershed for Laurentian faunas in general (Droser *et al.*, 1996). Thus, when considered critically, the trilobites of the Tourmakeady do not provide support for the notion of a special generative role for this particular insular fauna. However, such islands may have provided important refugia during times of global regression.

The closest biogeographic comparisons of the whole fauna are with illaenid-cheirurid biofacies faunas on the Laurentian palaeocontinent, and there is no reason to doubt that the South Mayo trough lay on the equatorial side of the Iapetus Ocean (Williams & Curry 1985). Similar conclusions were reached for the contemporary Dounans Limestone fauna (bathyurid biofacies) on the northern edge of the Midland Valley of Scotland (Ingham *et al.*, 1986). Amongst the Tourmakeady fauna there are several genera which are not confined to Laurentia, particularly those extending into Baltica: *Agerina*, *Celmus*, *Niobe*, *Illaeus*, *Nileus* and *Geragnostus*. Only two genera, *Protostygina* and *Geragnostus*, have Middle Ordovician Gondwanan records. The Baltic connections are of interest because the brachiopods (Williams & Curry 1985: 188) are stated to be quite different from those of that palaeocontinent.

SYSTEMATIC DESCRIPTIONS

REPOSITORY. Figured specimens are housed in the Sedgwick Museum, Cambridge (prefix SM) and the Natural History Museum, London (prefix It.).

Family **METAGNOSTIDAE** Jaekel, 1909
Genus **GERAGNOSTUS** Howell, 1935

TYPE SPECIES. *Agnostus Sidenbladhi* Linnarsson, 1869, from the Tremadoc of Sweden; by original designation.

Geragnostus clusus Whittington, 1963
Pl. 1, figs 10, 13–16; Pl. 2, fig. 9

MATERIAL. Assigned specimens It 25944–25948, 25961.

1963 *Geragnostus clusus* Whittington: 28–30, pl. 1, figs 1–17, text-fig. 3.

DISCUSSION. Whittington (1963) fully described this species from undistorted material from the Lower Head boulder. Because the terminal piece of the pygidium is longer than the postaxial field this species conforms to *Geragnostus* as opposed to *Arthrorhachis* in the revision of Fortey (1980). Cephalic shields of *Geragnostus* are all somewhat similar. Another closely similar form was figured by Ahlberg (1992) as *Geragnostus* sp. B, from the Lanna Limestone (Volkhov Stage) of Sweden. The pygidium is the more distinctive part of the exoskeleton. The best Irish pygidium (Pl. 1, fig. 16)

compares closely with that of the holotype (Whittington 1963: pl. 1, figs 1–6) in having the axis two-thirds the total pygidial length, while the terminal piece occupies two-thirds of the axial length. On the holotype, the terminal piece tapers backwards from the preceding part of the axis; however, on another of Whittington's specimens (1963: pl. 1, fig. 14) the terminal piece is slightly wider (tr.) than the second axial ring, as it is on the Tourmakeady specimen. Whittington (1965) commented on how closely similar *G. clusus* was to *G. longicollis* (Raymond, 1925) from the middle Table Head Formation. Possibly the only convincing difference was a more pronounced angulation in the cephalic outline of the former; this is not visible on the specimen of Pl. 1, fig. 15, which has been tectonically elongated, but is apparent on a less distorted specimen (Pl. 1, fig. 13). *Geragnostus clusus* seems to be the best name to apply to the Irish specimens.

Genus **DIVIDUAGNOSTUS** Koroleva, 1982

TYPE SPECIES. *Dividuagnostus minus* Koroleva, 1982; by original designation.

***Dividuagnostus* sp. indet.** Pl. 1, fig. 17

MATERIAL. Incomplete cephalic shield, It 25951.

DISCUSSION. A small headshield shows a transglabellar furrow with the form of a shallow inverted 'v'. This is typical of *Dividuagnostus* according to the revision of Zhou Zhi-yi (1987). The unusually large, triangular occipital lobes are also typical of this genus. Of species of Arenig age, the Irish specimen differs from *D. whitlandensis* (Fortey & Owens, 1987) in its wide cephalic border, but appears to be like *D. scotlandensis* (Whittard, 1966; see also Fortey & Owens 1987, fig. 17b–c) in the same feature. *Dividuagnostus scotlandensis* ranges through the Fennian Stage in South Wales. Without an associated pygidium the determination must be tentative.

Family **NILEIDAE** Angelin, 1854
Genus **NILEUS** Dalman, 1827

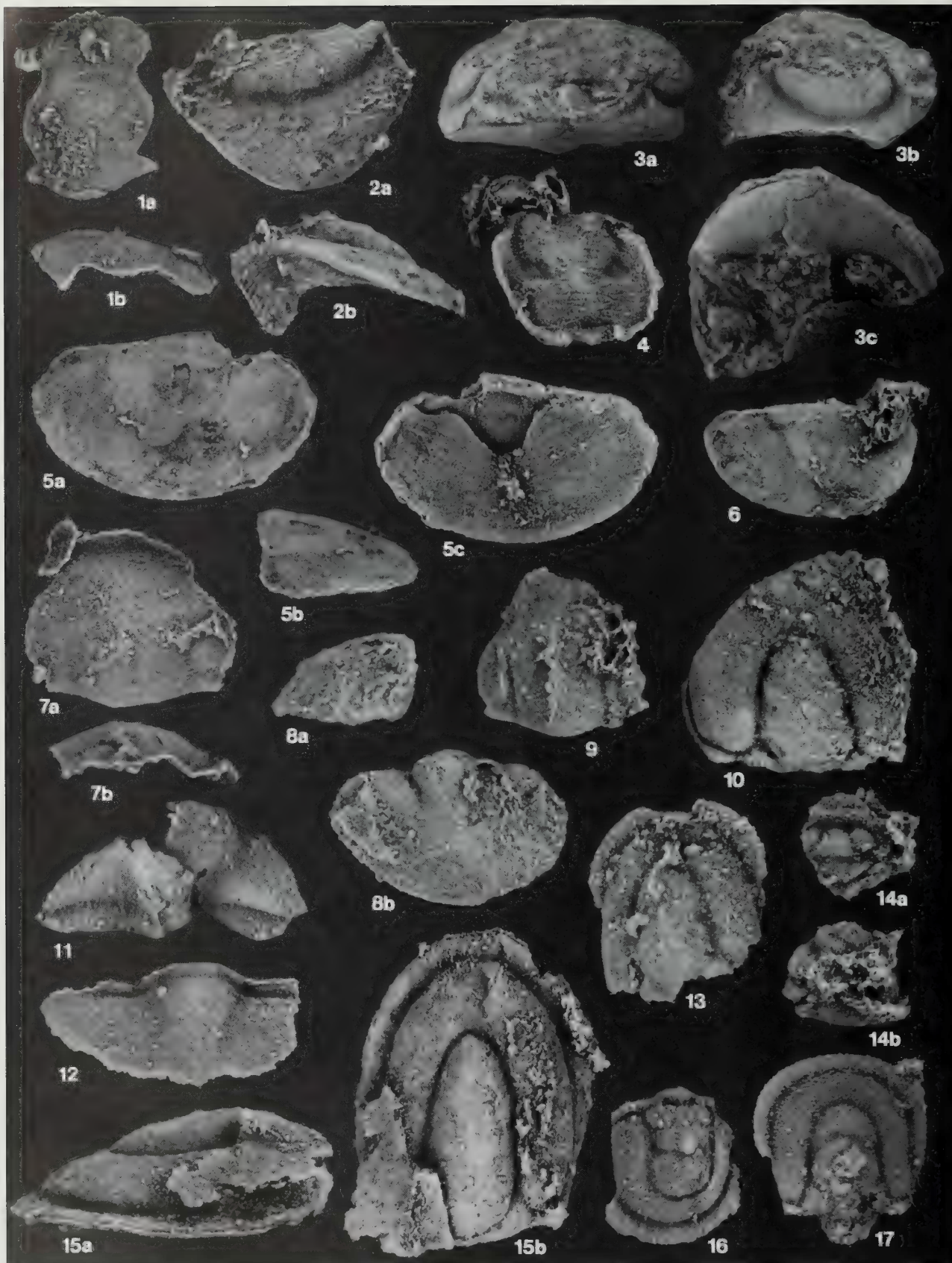
TYPE SPECIES. *Asaphus (Nileus) armadillo* Dalman, 1827, from the Arenig of Husbyfjöl, Skarpasen, Sweden; by monotypy.

***Nileus* sp.** Pl. 1, figs 1–6

MATERIAL. Assigned specimens It. 25935–25940, SM A10417.

DISCUSSION. The Tourmakeady species is similar to *Nileus affinis* from western Newfoundland (Whittington 1963, 1965). The specimens share similar posterior dimensions of the cephalic doublure (compare Pl. 1, fig. 3c with Whittington 1965: pl. 30, fig. 5); eyes of the same relative size and oblique inclination; hypostomes with narrow lateral rims (cf. Pl. 1, fig. 4 with Whittington 1965: pl. 31, fig. 6); pygidia with nearly identical shape and restriction of subdued dorsal terrace lines to the lateral margins; and pygidial doublure of nearly equal size with similar median embayment (cf. Pl. 1, fig. 5c with Whittington 1965: pl. 31, fig. 10).

The question of conspecificity cannot be evaluated with confidence given the few Irish specimens. The single cranidium recovered (Pl. 1, fig. 1a) is very narrow, but the specimen is a juvenile. Similarly, the Tourmakeady hypostome (Pl. 1, fig. 4) is nearly subquadrate, in contrast with the wider form known in *N. affinis*. The Irish specimen is small however, and lateral expansion with maturity can be observed in the ontogeny of various nileid hypostomes (e.g.,



Symphysurus arcticus Fortey, 1975a: pl. 21). On present evidence, the only feature that might indicate that the Irish material is distinct is a librigenal field that is smaller in area, particularly posteriorly, with the posterior section of the facial suture concomitantly shorter (Pl. 1, fig. 2a).

Family **RAPHIOPHORIDAE** Angelin, 1854

Genus **AMPYX** Dalman, 1827

Ampyx cf. *toxotis* Fortey, 1975a Pl. 1, figs 11, 12

MATERIAL. Assigned specimens It. 25949, 25950.

DISCUSSION. The Irish species, represented by only two specimens, shows strong similarity to *Ampyx toxotis* in its unusually long cranial posterior border, relatively small and sub-rounded glabella, effaced pygidial axis, and relatively deep furrow along the pygidial anterior margin. The species differ in that the cranial posterior border of the Irish species is not as exsagittally elongate, and the border furrow is better impressed, particularly proximally.

Family **STYGINIDAE** Vogdes, 1890

Genus **PROSTYGINA** Prantl & Pribyl, 1949

TYPE SPECIES. *Illaeus bohemicus* Barrande, 1872, Sarka Formation (Llanvirm), Czech Republic; by monotypy.

Protostygina coronula sp. nov.

Pl. 2, figs 1–6, 8

ETYMOLOGY. Latin, small crown.

DIAGNOSIS. Anterior border furrow long and relatively deep; axial furrows strongly impressed posteriorly; S0 well impressed; pygidial axis elevated sharply from pleurae; pygidium with sagittal length about 60% of maximum width.

HOLOTYPE. Cranidium, It. 25952 (Pl. 2, fig. 1); paratypes It. 25953–25958.

DESCRIPTION. This is based primarily on the largest adult specimens.

Cranidium with sagittal length subequal to, to very slightly longer than, the width (tr.) across midlength of palpebral lobes; maximum cranial width achieved across rear of posterior border; anterior sections of facial sutures subparallel immediately in front of palpebral lobes, then diverging slightly anteriorly; posterior sections of facial suture with strong (ca. 45 degrees from exsagittal plane) posterior divergence; anterior margin with strong anterior convexity; anterior border nearly flat, separated from front of glabella by

abrupt change in slope across trough-like anterior border furrow; border and border furrow of even length (sag.; exsag.) medially and laterally; axial furrows well impressed posteriorly, subparallel from S0 to opposite front of palpebral lobe, then diverging anteriorly; axial furrows effaced anteriorly opposite anterolateral corner of cranidium; preglabellar furrow absent, extent or presence of preglabellar field unknown; interocular fixigena large, with only weak dorsal convexity; palpebral furrow absent, palpebral lobe flat and grading directly into interocular fixigena; palpebral lobe narrow (tr.), elongate (exsag.); anterior glabellar furrows effaced; S0 shallow but well impressed, of similar length sagittally and exsagittally; L0 elongate (esp. sag.) and shelf-like, posterior margin with significant posterior convexity; L0 and rear of glabella with strong, arcuate dorsal convexity; posterior border narrow (tr.), only protruding laterally slightly past palpebral lobe; posterior border furrow very shallow; entire cranidium with very subdued dorsal sculpture of fine pits and small, low, anastomosing ridges.

Librigena, rostral plate, hypostome, and thorax unknown. Pygidium with sagittal length about 60% of maximum width; axis with maximum width about 75% of sagittal length; axis occupying about 60% of sagittal length of pygidium; anterior margin transversely straight within fulcrum, turned sharply posteriorly at fulcrum to run distally at about 45 degrees to transverse plane; posterior margin subcircular in outline; first pleural furrow defined adaxially to fulcrum, shallow but deepest adaxially; all other pleural and interpleural furrows completely effaced; articulating half ring very short (sag., exsag.); axial furrows extremely shallow, defined mainly as a sharp break in slope between pleura and axis, converging gently posteriorly, nearly transverse at rear to fully circumscribe somewhat blunt posterior of axis; five or six axial rings discernible on internal mold, but difficult to discern dorsally; ring furrows transverse and shallow on internal mold; entire pleural region lacking dorsal sculpture; double broad, of even width medially and laterally, reaching sagittally to rear of axis; relatively strong subparallel doublural terrace lines developed and progressively closer spaced on anterior half of double.

DISCUSSION. Fortey (1980: 56, 57) described an isolated cranidium from what is now recognized as the uppermost Ibexian (V_2) of Spitsbergen as *?Protostygina* sp. ind. This taxon is very similar to and definitely congeneric with *P. coronula* sp. nov. The species are distinguished mainly by the significantly deeper axial, anterior border, and occipital furrows of *P. coronula*. Fortey's suggestion that the Spitsbergen species (and hence the new Irish material) is related to *P. bohemia* (see Horny & Bastl (1970: pl. 8, fig. 3) remains the most tenable, despite the distorted internal mold preservation of the unique type specimen of that taxon. To the extent that evaluation is possible, *P. coronula* is distinguished from *P. bohemia* particularly by its longer pygidium with much more prominent axis. These features distinguish it also from the single exfoliated pygidium assigned to *Protostygina* sp. by Dean (1973;

PLATE 1

Figs 1–6 *Nileus* sp. **1a–b**, It. 25935, cranidium, dorsal and right lateral views, $\times 10$. **2a–b**, It. 25936, left librigena, external and ventrolateral views, $\times 10$.

3a–c, It. 25937, yolked librigenae-rostrum, anterior, right lateral, and ventral views, $\times 5$. **4**, It. 25938, hypostome, ventral view, $\times 10$. **5a–c**, It. 25939, dorsal, ventral, and left lateral views, $\times 10$. **6**, It. 25940, pygidium, dorsal view, $\times 7.5$.

Figs 7–9 *Benthampsis* sp. **7a–b**, It. 25941, cranidium, dorsal and right lateral views, $\times 15$. **8a–b**, It. 25943, pygidium, right lateral and dorsal views, $\times 15$. **9**, It. 25942, cranidium, dorsal view, $\times 15$.

Figs 10, 13–16 *Geragnostus clusus* Whittington, 1963 **10**, It. 25944, cephalic shield, dorsal view, $\times 10$. **13**, It. 25945, cephalic shield, dorsal view, $\times 15$.

14a–b, It. 25946, enrolled specimen, thoracic and right lateral views, $\times 15$. **15a–b**, It. 25947, cephalic shield, left lateral and dorsal views, $\times 10$. **16**, It. 25948, pygidium, dorsal view, $\times 15$.

Figs 11, 12 *Ampyx* cf. *toxotis* Fortey, 1975 **11**, It. 25949, cranidium, dorsal view, $\times 8.5$. **12**, It. 25950, pygidium, dorsal view, $\times 15$.

Fig. 17 *Dividuagnostus* sp. indet., It. 25951, cranidium, dorsal view, $\times 15$.

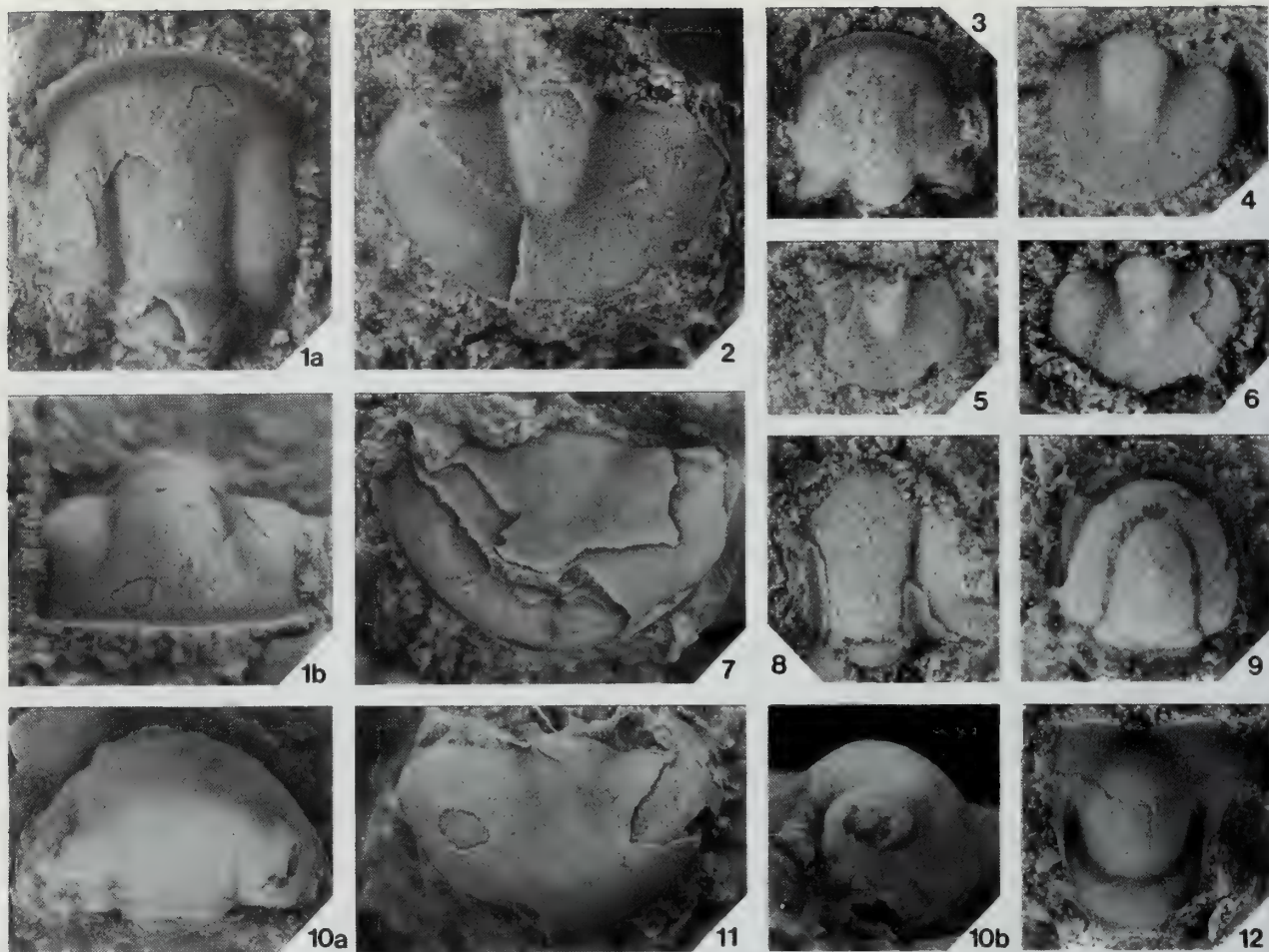


PLATE 2

- Figs 1–6, 8** *Protostygina coronula* sp. nov. **1a–b**, It. 25952, **holotype**, cranium, dorsal and anterior views, $\times 15$. **2**, It. 25953, pygidium, dorsal view, $\times 15$. **3**, It. 25954, cranium, dorsal view, $\times 15$. **4**, It. 25955, pygidium, dorsal view, $\times 15$. **5**, It. 25956, pygidium, dorsal view, $\times 15$. **6**, It. 25957, pygidium, dorsal view, $\times 15$. **8**, It. 25958, cranium, dorsal view, $\times 15$.
- Figs 7, 10–12** *Iliaenus weaveri* Reed in Gardiner & Reynolds, 1909 **7**, SM A10387, lectotype, pygidium, dorsal view, $\times 3.5$. **10a–b**, SM A10316, paralectotype, cranium and right librigena, dorsal and right lateral views, $\times 5$. **11**, It. 25959, pygidium, dorsal view, $\times 5$. **12**, It. 25960, hypostome, ventral view, $\times 10$.
- Fig. 9** *Geragnostus clusus* Whittington, 1963, It. 25961, cephalic shield, dorsal view, $\times 15$.

Sobova Formation, Upper Arenig, Turkey), although that specimen may well prove to be congeneric. *Protostygina adumbrata* Lisogor, 1995, is known from a single fragmentary cranium. The species, from the Llanvirn of Kazakhstan, is certainly congeneric with *P. coronula*, but detailed comparison will require more complete material.

Family **ODONTOPLEURIDAE** Burmeister, 1843
Subfamily **SELENOPELTINAE** Hawle & Corda, 1847
Genus **CERATOCEPHALINA** Whittington, 1956

TYPE SPECIES. *Ceratocephala (Ceratocephalina) tridens* Whittington, 1956, Edinburg Formation, lower Mohawkian, Virginia; by original designation.

Ceratocephalina ramskoeldi sp. nov.

Pl. 3, figs 9, 12; Pl. 4, figs 12–15

ETYMOLOGY. After Lars Ramsköld, University of Uppsala.

DIAGNOSIS. Cephalon with dense sculpture of fine tubercles; primary ontogenetic tubercles subdued and difficult to discern in holaspides; median occipital spine short; anterior border very short (sag; exsag.); slender genal spine continued on to librigenal field as interior border; border spines not distinct; epiborder furrow broad; epiborder spines small; pygidium with two marginal border spines and medial triangular projection.

HOLOTYPE. Cranium, It. 25987 (Pl. 4, fig. 9); paratypes It. 25972, 25973, 25988–25990.

DISCUSSION. The morphology and relationships of this species have been commented upon by Ramsköld (1991: 163), although material has not previously been illustrated. The taxon ranks among the oldest odontopleurids for which relatively good morphological information is available (see Ramsköld 1991 for a review of Arenig species). It appears to display a mixture of features of two



PLATE 3

Figs 1–3, 5 *Isocolus* sp. nov. A. **1**, It. 25962, cranidium, dorsal view, $\times 60$. **2**, It. 25963, cranidium, dorsal view, $\times 33$. **3**, It. 25964, cranidium, dorsal view, $\times 27$. **5**, It. 25965, pygidium, dorsal view, $\times 27$.

Fig. 4 *Catillicephalid* gen. et. sp. nov., It. 25966, cranidium, ventral view, $\times 23$.

Figs 6–8, 10, 11 *Illaeus weaveri* Reed in Gardiner & Reynolds, 1909 **6**, It. 25967, pygidium, dorsal view, $\times 23$. **7**, It. 25968, left librigena, external view, $\times 23$. **8**, It. 25969, transitory pygidium, dorsal view, $\times 35$. **10**, It. 25970, hypostome, ventral view, $\times 23$. **11**, It. 25971, cranidium, dorsal view, $\times 33$.

Figs 9, 12 *Ceratocephalina ramskoeldi* sp. nov. **9**, It. 25972, cranidium, dorsal view, $\times 30$. **12**, It. 25973, pygidium, dorsal view, $\times 17$ (see also Pl. 4, fig. 15).

Fig. 13 Unassigned hypostome A, It. 25974, ventral view, $\times 33$.

Figs 14, 15 Unassigned hypostome B. **14**, It. 25975, ventral view, $\times 23$. **15**, It. 25976, ventral view, $\times 23$.

odontopleurid subfamilies, resembling Ceratocephalinae Richter & Richter, 1925, in pygidial details and Selenopeltinae in cephalic morphology. If Ramsköld's (1991: 166–168) character analysis is correct, however (and it is followed herein), *Ceratocephalina ramskoeldi* can be assigned with confidence as possibly the most primitive representative of Selenopeltinae. The following discussion is based primarily on Ramsköld's work.

The pygidium of *Ceratocephalina ramskoeldi* differs from those of all other assigned selenopeltines in the marginal position of its lateral border spines. In typical selenopeltines, these spines are supramarginal. The median area of the posterior margin is also distinctly triangular and drawn posteriorly, nearly into a median spine. In these features, the sclerite agrees with the pattern of three marginal spines characteristic of Ceratocephalinae. Ramsköld (1991) interpreted this pattern as plesiomorphic and probably general to a clade encompassing both subfamilies. Hence, the median area of the *C. ramskoeldi* pygidium possibly reflects a transition from a primitive median-spined condition to the arcuate condition with a fringe of small accessory spines seen in Selenopeltinae. The lateral spines are similarly in a plesiomorphic marginal position, and have not yet begun to migrate dorsally to the position apomorphic for the bulk of Selenopeltinae. The cephalic morphology of *C. ramskoeldi* is much less ambiguous. The presence of a very short (sag., exsag.) anterior border lacking spines or tubercles and of a slender genal spine base that overhangs and is not confluent with the posterior and exterior borders, but rather which runs onto the interior border on the field, are both basal selenopeltine apomorphies. In addition, the species bears none of the apomorphies of Ceratocephalinae (e.g., the third glabellar spine pair is not set atop an independently inflated swelling of the glabella).

Ceratocephalina ramskoeldi is most similar to *C. trispineus* (Young, 1973) from the Ibexian (Zone H) of Utah. *C. ramskoeldi* differs from the Utah species in the possession of denser, finer tuberculate sculpture; a shorter (sag., exsag.) anterior border; more prominently inflated L1 and L2; more deeply incised S0; a relatively shorter median occipital spine; broader librigenal field; and genal spine with a narrower base. As noted by Ramsköld (1991), the pygidia assigned by Young (1973) to *C. trispineus* are not those of an odontopleurid; they belong in fact to a pilekiid.

The single fragmentary cranium described by Fortey & Droser (1996: 98, fig. 7.8) as *Diacanthaspis* sp. is also a primitive *Ceratocephalina*. It is more similar to *C. trispineus* than to *C. ramskoeldi* in the prominence of its anterior cranial border, but is distinguished from both by its much more robust dorsal tuberculation.

Family ISOCOLIDAE Angelin, 1854

DISCUSSION. As presently conceived, Isocolidae is restricted to the Middle and Upper Ordovician, and the Tourmakeady species, described below, is the oldest known member of the family. However, Fortey (1983) and Ingham (*in Ingham et al.* 1986) have

established the Ibexian presence of a group of genera similar to Sunwaptan forms currently assigned to the family Catillicephalidae. This latter record is herein extended to the basal Whiterockian (see below). These catillicephalids have so much in common with the isocolids that there is a strong likelihood they are phylogenetically related. The familial distinction between them may prove artificial. However, Catillicephalidae is itself in need of phylogenetic revision, and it remains to be established whether the Sunwaptan/Ibexian genera are related to several pre-Sunwaptan genera, including *Catillicephal* itself. Pending a comprehensive cladistic review of the problems, we follow traditional usage and retain separate families.

Genus ISOCOLUS Angelin, 1854

TYPE SPECIES. *Isocolus Sjögreni* Angelin, 1854, from the Boda Limestone (Ashgill) of Dalarna, Sweden; by monotypy.

Isocolus sp. nov. A

Pl. 3, figs 1–3, 5; Pl. 4, figs 7, 8, 10, 11

MATERIAL. Assigned specimens It. 25962–25965, 25983–25986.

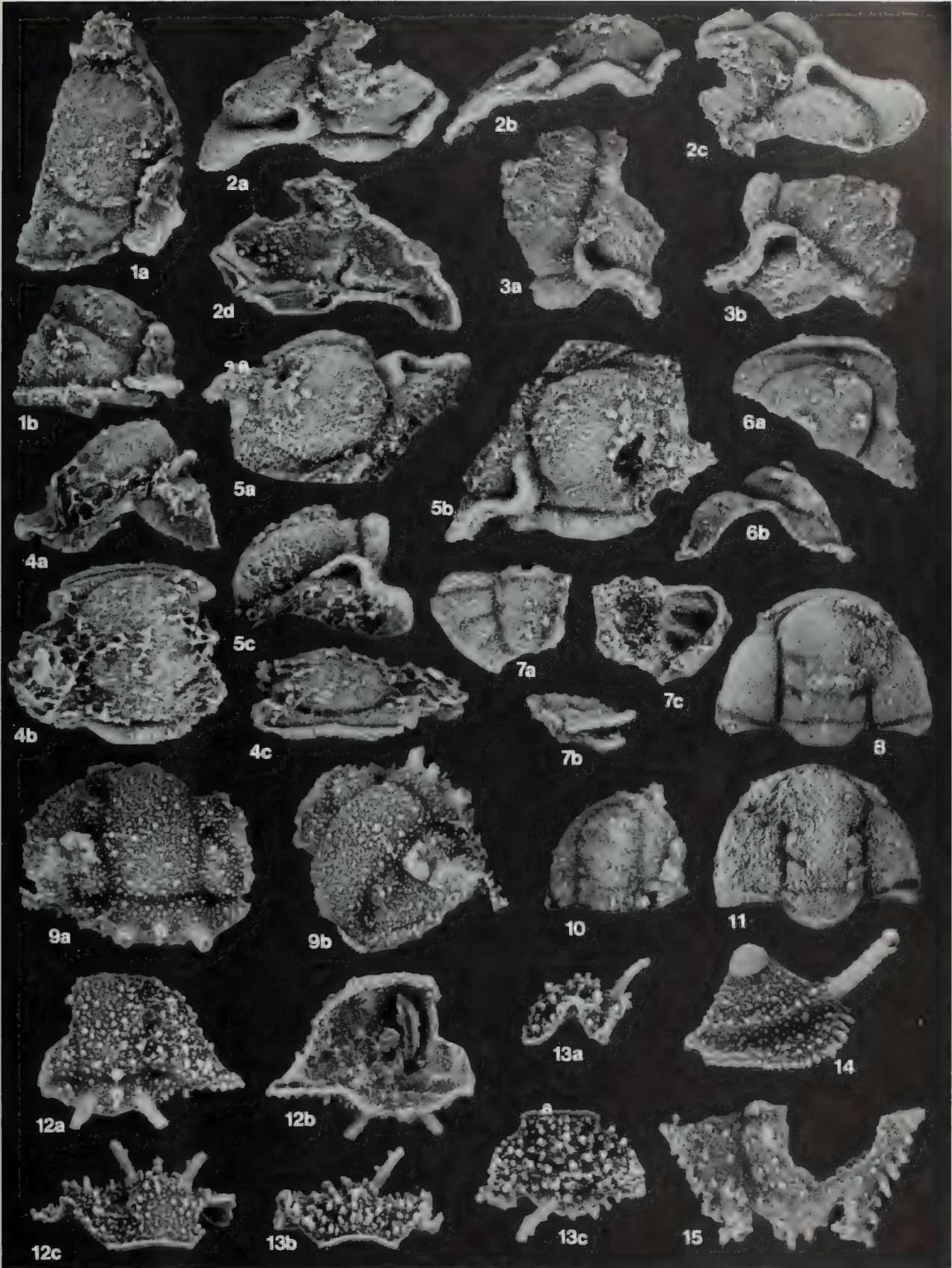
DESCRIPTION. Cranium with sagittal length about 75% of maximum width across posterior border and subequal to width across palpebral lobes; anterior margin of anterior border with gentle, even anterior convexity; anterior border very short (sag., exsag.); anterior border furrow sharply incised but extremely short (sag., exsag.); glabella widest anteriorly, maximum width about 80% of sagittal length excluding L0; preglabellar field very short, expanded laterally into narrow frontal area with considerable dorsal convexity; glabella laterally concave, axial furrows bowed inwards; S1 and S2 deeply incised and slot-like, deeper and longer (exsag.) proximally than distally near contact with axial furrow, lengthened into pitlike form at proximal end, declined posteriorly at about 30 degrees from transverse plane; S3 faint and transversely aligned, contacting axial furrow just behind eye ridge; anteromedian lobe of glabella slightly swollen and anteriorly expanded; L1 and L2 trapezoidal in outline; dorsal glabellar sculpture lacking; S0 much shorter (exsag.) than S1 and S2, evenly incised both medially and laterally, with very shallow 'W' shape, anteriorly convex medially; L0 longest medially, shortened significantly behind L1, transversely convex, but sagittally nearly flat-topped, median node very faint; narrow area of fixigena present opposite contact of axial and preglabellar furrow and in front of eye ridge; eye ridge faint, slightly declined posteriorly, relatively broad (tr.); palpebral lobe tiny; anterior sections of facial sutures very short (exsag.), subparallel in front of palpebral lobes, converging anteriorly; posterior sections of facial sutures with strong initial posterior divergence behind palpebral lobes, then more gentle divergence posteriorly; posterior fixigena with considerable area, moderate dorsal inflation, and lacking dorsal sculpture; posterior border furrow nearly straight, length (exsag.) similar along most of width, lengthening slightly abaxially; posterior border very short proximally, lengthening greatly distal to fulcrum. Pygidium incompletely

PLATE 4

Figs 1–6 Catillicephalid gen. et sp. nov. **1a–c**, It. 25977, cranium and right librigena, oblique, right lateral, and left lateral views, $\times 15$. **2a–d**, It. 25978, cranium, dorsal, posterodorsal, oblique, and ventral views, $\times 15$. **3a–b**, It. 25979, cranium, dorsolateral and oblique views, $\times 15$. **4a–b**, It. 25980, cranium, anterodorsal, left lateral, and dorsal views, $\times 15$. **5a–b**, It. 25981, cranium, dorsal and right lateral views, $\times 15$. **6a–b**, It. 25982, cranium, dorsal and anterior views, $\times 15$.

Figs 7, 8, 10, 11 *Isocolus* sp. nov. **A**. **7a–c**, It. 25983, pygidium, dorsal, ventral, and left lateral views, $\times 15$. **8**, It. 25984, cranium, dorsal view, $\times 15$. **10**, It. 25985, cranium, dorsal view, $\times 15$. **11**, It. 25986, articulated exoskeleton (destroyed after photography), dorsal view of cephalon, $\times 15$.

Figs 9, 12–15 *Ceratocephalina ramskoeldi* sp. nov. **9a–b**, It. 25987, **holotype**, cranium, dorsal and oblique views, $\times 15$. **12a–c**, It. 25988, cranium, dorsal, ventral, and anterior views, $\times 15$. **13a–c**, It. 25989, cranium, left lateral, anterior, and dorsal views, $\times 15$. **14**, It. 25990, left librigena, external view, $\times 12$. **15**, It. 25973, pygidium, dorsal view, $\times 15$ (see also Pl. 3, fig. 12).



known; sagittal length approximately 60% of maximum width; axis with width about 70% of sagittal length; first three pleural furrows deeply incised; interpleural furrows nearly obscure; articulating half-ring set off from axis by prominent ring furrow; posterior axial rings and ring furrows difficult to discern; subdued but definite pygidial border developed around margin; posterior margin evenly arcuate; lateral and posterior aspects of cranium defined as subvertical wall (Pl. 4, fig. 7b), which is turned out again in a second, ventral, marginal rim; doublure relatively broad.

DISCUSSION. We have not formally named this species because the two best cranidia (Pl. 4, figs 8, 11) were lost or broken following photography, and there are no replacement specimens suitable to serve as types.

The Tourmaeade species is obviously related to previously described species of *Isocolus*, indicated particularly by the slot-like glabellar furrows that are greatly shallowed adaxial to the contact with the axial furrow. However, the laterally concave glabella of the Irish form is unique in the entire group. Other autapomorphic features include the apparently lacking dorsal sculpture, versus prominent raised lines in other species, the significantly broader posterior fixigena, and the posterolaterally directed, versus subtransverse, glabellar furrows.

The ventral morphology of the *Isocolus* pygidium has not previously been described. The Irish material reveals the unexpected presence of a vertically oriented wall beneath what appears dorsally to be the pygidial margin. This 'wall' is flared ventrally into a second, ventral rim (Pl. 4, fig. 7b). Reference to articulated material (Whittington 1956, 1963) indicates the larger, dorsally placed rim is almost certainly the true pygidial margin, and not analogous to the fulcral processes, rim, or spines often seen in groups like Entomaspidae Ulrich in Bridge, 1931 (e.g., Ludvigsen & Westrop in Ludvigsen *et al.*, 1989). The ventral wall and rim may therefore be doublural in origin.

Family CATILLICEPHALIDAE Raymond, 1937

DISCUSSION. See remarks under discussion of Isocolidae above.

Catillicephalid gen. et sp. nov. Pl. 3, fig. 4; Pl. 4, figs 1–6

MATERIAL. Assigned specimens It. 25966, 25977–25982.

DISCUSSION. The forward-expanding glabella, very short preglabellar field, tiny palpebral lobe set near to the axial furrow, anterior eye position, broad posterior fixigena, and distally elongated (exsag.) posterior cranial border all indicate relationship of this unusual Irish species to Sunwaptan-Ibexian forms presently assigned to Catillicephalidae. The size and attitude of the posterior border as well as the position and inclination of S1, position and size of the palpebral lobe, and size of the cephalic border are further similarities to the stratigraphically nearest species, i.e. *Distazeris adoceta* Ingham (in Ingham *et al.*, 1986), from the Highland Border Complex of Scotland (Pratt 1992: 73 has criticized the generic assignment of this species).

The Irish species possesses a feature that distinguishes it from all related taxa, and apparently from all other trilobites: the development at the junction of the axial, posterior border, and occipital furrows of an exoskeletal hood that encloses a cone-shaped space opening laterally. The homology of this structure is very difficult to determine. The posterior border furrow runs directly into it, and appears to terminate beneath the hood (Pl. 4, fig. 2d). The occipital furrow meets the axial furrow on the adaxial side of the hood, and the junction of these furrows continues to circumscribe the hood posteriorly (Pl. 4, fig. 2b).

Family ILLAENIDAE Hawle & Corda, 1847

Genus *ILLAENUS* Dalman, 1827

TYPE SPECIES. *Entomostracites crassicauda* Wahlenberg, 1818, p. 27, from the Llandeilo of Fjäckå, Dalarna, Sweden; by subsequent designation of Pictet (1854: 515).

Illaeus weaveri Reed in Gardiner & Reynolds, 1909

Pl. 2, figs 7, 10–12; Pl. 3, figs 6–8, 10, 11;

Pl. 5, figs 1–11; Pl. 6, figs 1–12

1909 *Illaeus weaveri* Reed in Gardiner & Reynolds: 142, pl. 6, figs 1–3.

1910 *Illaeus weaveri* Reed in Gardiner & Reynolds: 272.

1945 *Illaeus weaveri* Reed: 63.

1968 *Illaeus weaveri* Reed; Whittington: 56.

1988 *Illaeus weaveri* Reed; Morris: 115.

DIAGNOSIS. Terrace lines on rear of cranium, restricted to anterior part of librigenal field; librigenal flange only moderately developed; vincular furrow only impressed posteriorly on librigenal doublure; pygidium with sagittal length 55–60% of maximum width.

MATERIAL. Lectotype, selected here, SM A10387, pygidium (Pl. 2, fig. 7), original of Reed in Gardiner & Reynolds (1909, pl. 6, fig. 2); paralectotype SM A10316, cranium and right librigena (Pl. 2, fig. 10); topotypes It. 25959, 25960, 25967–25971, 25992–26014.

DESCRIPTION. Due to the varying amounts and vectors of distortion of much of the available material, measured ratios are approximate at best. The large pygidium of Pl. 6, fig. 7, is considered to be nearly undistorted, and pygidial ratios are based upon this specimen.

Cranidium with length (sag., measured in sagittal profile) 75–88% of maximum width across midlength (exsag.) of palpebral lobes; maximum anterior width about 90% of width across palpebral lobes; posterior sections of facial sutures declined nearly vertically when palpebral lobe is oriented in horizontal plane, diverging sharply posteriorly, nearly transverse; anterior sections of facial suture declined at about 30 degrees from horizontal when palpebral lobe is oriented in horizontal plane, slightly anteriorly divergent immediately in front of palpebral lobe, then forming even, laterally convex arc to converge near anterior margin; palpebral lobes relatively large and elongate; axial furrow strongly effaced, impressed only posteriorly, behind midlength of palpebral lobe; entire cranium

PLATE 5

Figs 1–11 *Illaeus weaveri* Reed in Gardiner & Reynolds, 1909 **1a–b**, It. 25992, cranium and left librigena, anterior and left lateral views, $\times 10$. **2a–b**, It. 25993, cranium and right librigena oblique and anterior views, $\times 4.5$. **3a–c**, It. 25994, cranium, dorsal, anterior, and left lateral views, $\times 7.5$. **4a–c**, It. 25995, cranium, dorsal, anterior, and right lateral views, $\times 10$. **5a–c**, It. 25996, cranium, dorsal, anterior, and left lateral views, $\times 15$. **6**, It. 25998, rostral plate, ventral view, $\times 10$. **7a–b**, It. 25997, rostral plate, ventral and dorsal views, $\times 7.5$. **8a–b**, It. 25999, rostral plate, posterior and ventral views, $\times 10$. **9a–b**, It. 26000, cranium, dorsal and anterior views, $\times 15$. **10a–c**, It. 26001, cranium, dorsal, anterior, and left lateral views, $\times 15$. **11**, It. 26002, cranium, ventral view, $\times 10$.



vaulted, maximum sagittal curvature achieved slightly posterior to slightly anterior of palpebral lobes; anterior border and border furrow not evident; prominent terrace lines running subparallel to anterior margin, finer and more closely spaced near margin, coarser and more widely spaced dorsally; fine subparallel, transverse terrace lines developed across rear of glabella, occipital region, and rear of palpebral lobes, originating with close spacing laterally, spacing greater sagittally, forming ellipsoid pattern (Pl. 5, fig. 3a); occipital and posterior border doublure very short (sag., exsag.).

Librigena with prominent, closely spaced terrace lines on antero-lateral aspect; coarser lines matching those on cranidium only expressed on anterior part of field; posterolateral librigenal corner broadly lobate, ventrolateral margin bowed in, single prominent terrace line forming sharp posterolateral rim; field with moderate dorsal convexity, sculpture excluding anterior terraced lines smooth; posterior margin with strong posterior convexity; eye relatively large, exsagittal length slightly more than twice the width (tr.), doublure broad and robust; vincular furrow strong posteriorly beneath posterolateral corner, becoming effaced anteriorly.

Rostral plate subtrapezoidal; length (sag.) 40% of width; anterior margin with gentle, even anterior convexity; posterior margin nearly transverse, with slight sagittal posterior bulge; connective sutures obliquely inclined at about 45 degrees, laterally concave; ventral aspect with prominent, coarse, terraced lines, larger and more widely spaced (sag., exsag.) anteriorly; reentrant dorsal flange incompletely known, but robust.

Hypostome with sagittal length about 80% of maximum width across anterior wings; anterior margin (hypostomal suture) with lobate 'M' shape; anterior wings broad and nearly spatulate; wings grading into middle body posteriorly, but separated anteriorly by trough-like furrow delineating anterior part of body; lateral border narrow, sharply defined and ridge-like; lateral border furrow narrow and deeply incised; middle furrow deep, deepest laterally, fully impressed medially, with strong posterior curvature; middle body moderately inflated, lacking sculpture; maculae small but prominent, set just behind middle furrow; lateral border furrow grading without interruption into posterior border furrow; lateral border grading without interruption into posterior border; posterior border with posterior convexity nearly identical to that of middle furrow.

Thoracic segments poorly known; articulating half ring and ring furrows not discernible; axial furrow defined only as break in slope from pleura; axis with broad transverse convexity; prominent fulcrum on pleural lobe, 70–80% distance abaxially.

Pygidium with length (sag.) 55–60% of maximum width; axis with anterior width just under 40% of pygidial width; anterior margin transversely straight between fulcra; fulcrum set at 75% of distance between sagittal plane and lateral margin; prominent, subtriangular articulating facet forming obliquely inclined, anterolaterally directed plane distal to fulcrum; posterior margin nearly semicircular in plan view, subelliptical in posterodorsal view; pygidium with sagittal profile nearly flat anteriorly, prominently vaulted posteriorly, set at nearly 90 degrees to anterior part posteriorly near margin; plane of margin declined about 10 degrees from that of

anterior flat part of sagittal profile; axis only slightly raised from pleura, becoming increasingly less differentiated posteriorly; doublure broad, extended forward to rear of axis (about 60% of sagittal length from front of pygidium); doublure notched medially around termination of axis, protruding forward on either side of axis, then evenly arcuate distally.

DISCUSSION. *Iliaenus weaveri* belongs to Jaanusson's (1957: 110) *I. sarsi* group, which includes the taxa *I. consimilis* Billings, 1865, *I. fraternus* Billings, 1865 (see Whittington 1965 for both), *I. auriculatus* Ross, 1967, and *I. oscitatus* Fortey, 1980 (see also Nielsen 1995). The group is characterized particularly by the form of the pygidial doublure, with its median notch flanked by anterior projections (e.g., Pl. 6, fig. 12), and all species show to greater or lesser extent the development of posterolateral 'flanges' on the librigenae.

Iliaenus weaveri is perhaps most similar to *I. auriculatus*, from the basal Whiterockian (Zone L) of the Antelope Valley Limestone, Pyramid Peak, California. However, the species differ in that *I. weaveri* has a relatively longer pygidium, much less pronounced medial pygidial doublural notching, a rostral plate that is much longer medially, and librigena with a less pronounced lateral flange. The vincular furrow of *I. weaveri* is restricted to the posterior part of the librigenal doublure (Pl. 6, figs 3b, 4b), whereas that of *I. auriculatus* is continued anteriorly (Ross 1967: pl. 5, fig. 29).

Iliaenus weaveri differs from *I. oscitatus*, from the Whiterockian of Spitsbergen, in the lack of that species' prominently pitted sculpture and fully defined cranial anterior border. Additionally, the cranial sagittal profile of *I. oscitatus* is much more evenly convex than that of *I. weaveri* (compare Fortey 1980: pl. 10, figs 2, 6, with Pl. 5, figs 3c, 4c, 5c).

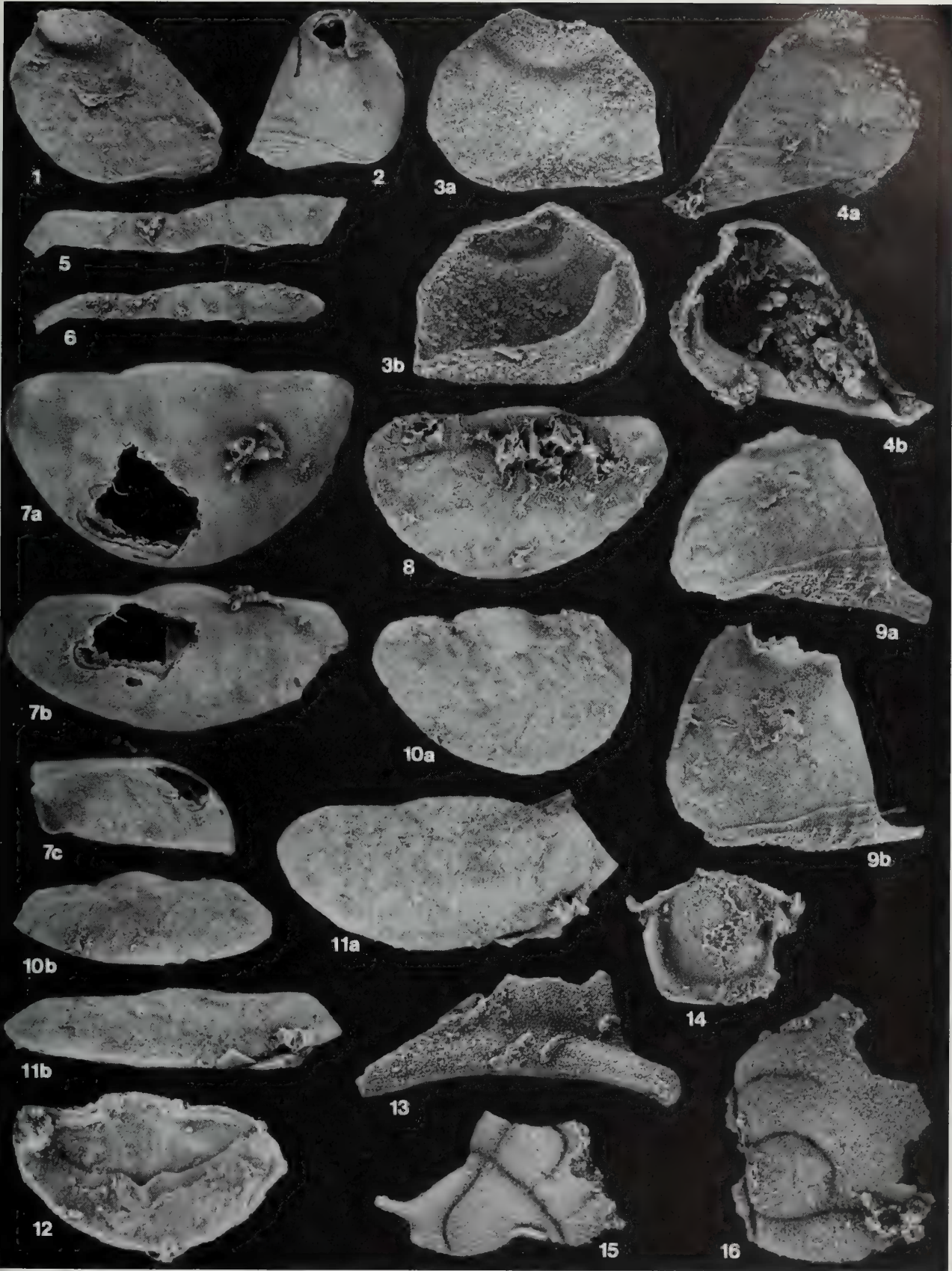
Both *I. consimilis* and *I. fraternus*, from the Whiterockian of Newfoundland, are distinguished from *I. weaveri* in the possession of prominent terrace lines over the entirety of their dorsal surface, including medially on the cranidium, on the librigenal field, and on all of the pygidial axial and pleural region. The size and shape of the librigenal flange of *I. fraternus*, however, is similar to that of *I. weaveri* (e.g., Whittington 1965: pl. 45, fig. 17).

Family CHEIRURIDAE Hawle & Corda, 1847 Subfamily uncertain

DISCUSSION. Cheirurid subfamilial classification is in a state of flux. Several subfamilies (including Cheirurinae, Acanthoparyphinae, Heliomerinae, and Deiphoninae) are undoubtedly monophyletic. Others (e.g., Eccoptochilinae, Sphaerexochinae, Cyrtometopinae, Areiinae) are more problematic, and their status as natural groups has yet to be convincingly established. Two of the genera dealt with herein (*Kawina* Barton, and *Mayopyge* gen. nov.) would be assigned, by current convention, to the subfamily Sphaerexochinae. This taxon, however, is particularly problematic because *Sphaerexochus* itself is a highly autapomorphic genus, the sister

PLATE 6

Figs 1–12 *Iliaenus weaveri* Reed in Gardiner & Reynolds, 1909 **1**, It. 26003, right librigena, external view, $\times 7.5$. **2**, It. 26004, left librigena, external view, $\times 5$. **3a–b**, It. 26005, right librigena, external and internal views, $\times 10$. **4a–b**, It. 26006, left librigena, external and internal views, $\times 7.5$. **5**, It. 26007, thoracic segment, dorsal view, $\times 5$. **6**, It. 26008, thoracic segment, dorsal view, $\times 5$. **7a–c**, It. 26009, pygidium, dorsal, posterior, and left lateral views, $\times 3.5$. **8**, It. 26010, pygidium, dorsal view, $\times 5$. **9a–b**, It. 26011, right librigena, ventrolateral and external views, $\times 10$. **10a–b**, It. 26012, pygidium, dorsal and posterior views, $\times 7.5$. **11a–b**, It. 26013, pygidium, dorsal and posterior views, $\times 5$. **12**, It. 26014, pygidium, ventral view, $\times 10$. **Figs 13–16** *Kawina divergens* (Reed, 1945). **13**, It. 26015, left librigena, external view, $\times 6.5$. **14**, It. 26016, hypostome, ventral view, $\times 10$. **15**, It. 26017, cranidium, oblique view, $\times 10$. **16**, It. 26018, cranidium, dorsal view, $\times 10$.



taxon of which is unknown. Until such time as we are able to base the subfamilial classification of such genera on explicit and well-supported hypotheses of cladistic relationship, we prefer to regard their subfamilial affinities as uncertain.

Genus *KAWINA* Barton, 1916

Cydonocephalus Whittington, 1963: 97.

TYPE SPECIES. *Cheirurus vulcanus* Billings, 1865, from the Cow Head Group (lower Whiterockian), western Newfoundland; by original designation.

DISCUSSION. Whittington (1963: 97) distinguished his new *Cydonocephalus* (type species *C. griphus* Whittington, 1963, lower Whiterockian, western Newfoundland) from *Kawina* Barton, 1916, on the assertion that the 'glabella is most convex anteriorly (not posteromedially) and juts forward, lobe 1p, and in some species 2p and 3p, are gently inflated, and occipital furrow curves forward (not back) medially.' Of these features, only the glabellar convexity holds for all six of the western Newfoundland species assigned to *Cydonocephalus*. The glabellar lobes of large specimens of *C. torulus* Whittington, 1963, are not markedly more inflated than those of *Kawina vulcanus* (Billings, 1865) (compare Whittington 1963: pl. 28, figs 5, 16), and the occipital furrows of both *C. torulus* and *C. griphus* both clearly curve backward (Whittington 1963: pl. 27, figs 3, 10, 13, 16; pl. 28, figs 1, 5; pl. 29, figs 1, 4).

All of the pygidia (Whittington 1963: pl. 31) which likely belong to species assigned by Whittington to *Cydonocephalus* have their pleural ribs fused along almost their entire length. *Kawina arnoldi* Whittington, 1963, however, has ribs with distally free tips (Whittington 1963: pl. 26, fig. 14). This is similar to the Irish species (Pl. 7, fig. 2), the pygidium of which differs from that of *K. arnoldi* only in proportions. However, the sagittal profile of the Irish cranidia is obviously like that of *Cydonocephalus*, with the point of maximum convexity anterior, not posterior. *Kawina arnoldi*, however, lacks the strong posterior convexity of the type species, and has a nearly evenly arcuate sagittal cranial profile (Whittington 1963: pl. 26, fig. 8).

Considering all the species it is not possible to specify synapomorphic characters that would distinguish the two genera as separate monophyletic groups. Rather, species presently assigned to one or the other show overlapping variation in characters considered by Whittington to be diagnostic of *Cydonocephalus*, as well as in pygidial morphology. For these reasons, *Cydonocephalus* is placed in subjective junior synonymy of *Kawina* herein.

Kawina divergens (Reed, 1945)

Pl. 6, figs 13–16; Pl. 7, figs 1–5, 7

- 1909 *Pliomera* aff. *fischeri* (Eichwald); Reed in Gardiner & Reynolds: 144; pl. 6, fig. 4.
- 1925 *Kawina* sp., Raymond: 144.
- 1945 *Kawina divergens* Reed: 59.
- 1971 *Kawina?* *divergens* Reed; Lane: 56; text-fig. 9a.
- 1988 *Kawina?* *divergens* Reed; Morris: 119.

DIAGNOSIS. Dorsal sculpture of very fine, densely spaced granules; short, thorn-like genal spine retained in large holaspides; glabella with nearly even sagittal convexity, point of maximum convexity anterior; pygidium wide, with splayed, subquadrate ribs bearing free tips.

HOLOTYPE. Pygidium, SM A10396 (Pl. 7, fig. 2); topotypes It. 26015–26022, 26200.

DESCRIPTION. Cranidium with sagittal length 70–75% of maximum width across posterior border; glabella with width across midlength (exsag.) of L2 subequal to or slightly narrower than width across midlength of L1; maximum glabellar width subequal to length (measured in sagittal profile) excluding L0; anterior border short but complete medially; preglabellar furrow deeply incised, grading abaxially into axial furrow of similar depth; anterior fixigena a narrow, laterally convex strip, widest opposite midlength (exsag.) of L3, narrowing posteriorly in front of palpebral lobe; palpebral lobe narrow, entirely set off from interocular fixigena by very sharply incised palpebral furrow; interocular fixigena broadening posteriorly, smooth, with moderate dorsal convexity; interocular fixigena grading smoothly into broad posterior fixigena, held in plane declined about 60 degrees from horizontal; anterior sections of facial sutures short (exsag.), parentheses-shaped, with strong anterior convergence from midlength of L3 to front of glabella; glabella strongly inflated, sagittal profile with nearly even dorsal convexity, slightly more pronounced anteriorly; S1 nearly transverse distally, curved in nearly subcircular arc proximally, similar in depth to axial furrow but shallowing abruptly in front of S0 so that L1 is not quite fully isolated; L1 with only slight independent inflation, length (exsag.) subequal to width (tr.); S2 similar distally to S1, proximal part shorter and less posteriorly inclined; L2 with no independent inflation, length (exsag.) 80–85% of that of L1; S3 as deeply incised as S1 and S2, but not reaching as far adaxially, with less posterior curvature, and shallowed slightly near contact with axial furrow; L3 with slight anterolateral inflation, length about 80% of that of L2; frontal glabellar lobe with slight lateral inflation immediately anterior to S3, anterior margin with blunt anterior convexity; S0 composed of three distinct posteriorly bowed regions, two lateral ones behind L1, and a medial one between the L1 lobes, depth similar to axial furrow, medial region slightly longer (sag., exsag.) than lateral parts (exsag.); L0 similar in length to distal parts of posterior border, with nearly flat top in sagittal profile; posterior border sharply incised, very short (exsag.), and running nearly transversely to genal angle, where it is bowed anteriorly; posterior border very short proximally, but lengthening greatly distal to fulcrum to form lobate genal angle; short, thornlike, subtriangular genal spine retained on even largest specimens; entire dorsal cranial surface with very fine, unimodal granular sculpture.

Librigena poorly known; field and lateral border both with fine granular sculpture similar to that of cranidium; lateral border well defined posteriorly, but grading into field anteriorly; lateral border furrow with concomitant shallowing anteriorly; field apparently quite narrow (tr.); eye unknown.

Rostral plate unknown. Hypostome with sagittal length 75% of maximum width across anterior wings; width across shoulders 80% of width across anterior wings; width across posterolateral corners two thirds that across anterior wings; anterior margin (hypostomal suture) with strong anterior convexity; sharp marginal rim and furrow developed laterally, middle body extended to margin medially; strong antennular notch between shoulder and anterior wing; lateral border broad and inflated, with fine granular sculpture; lateral border furrow shallow and broad (tr.); posterior margin with only slight posterior convexity; posterior border and posterior border furrow similar in dimensions to lateral border and furrow; middle body with sagittal length slightly greater than maximum width, moderate ventral inflation, strongest anteriorly; sculpture of fine granules somewhat more subdued than that of lateral border; middle furrow impressed only laterally, strongly declined posteriorly.

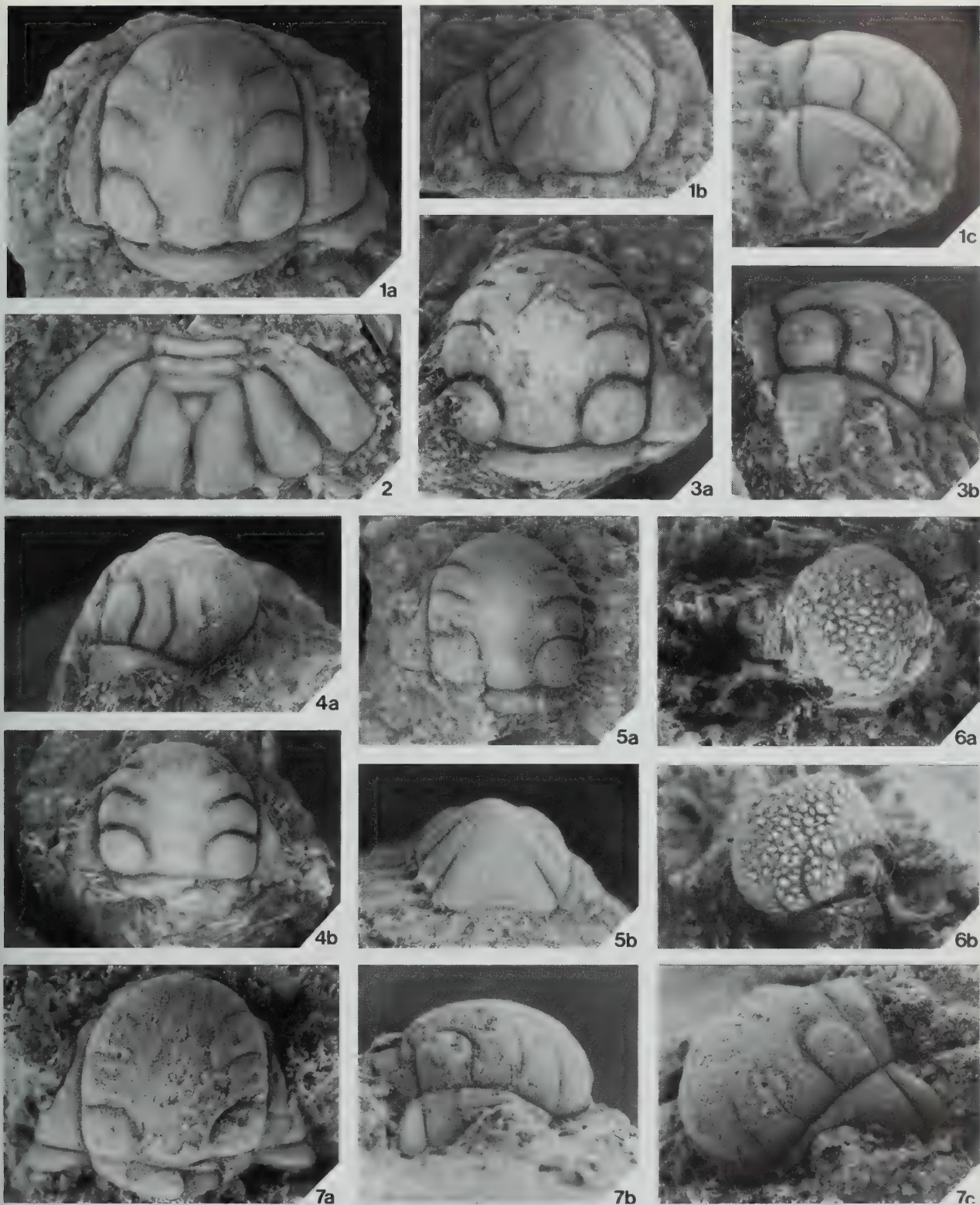
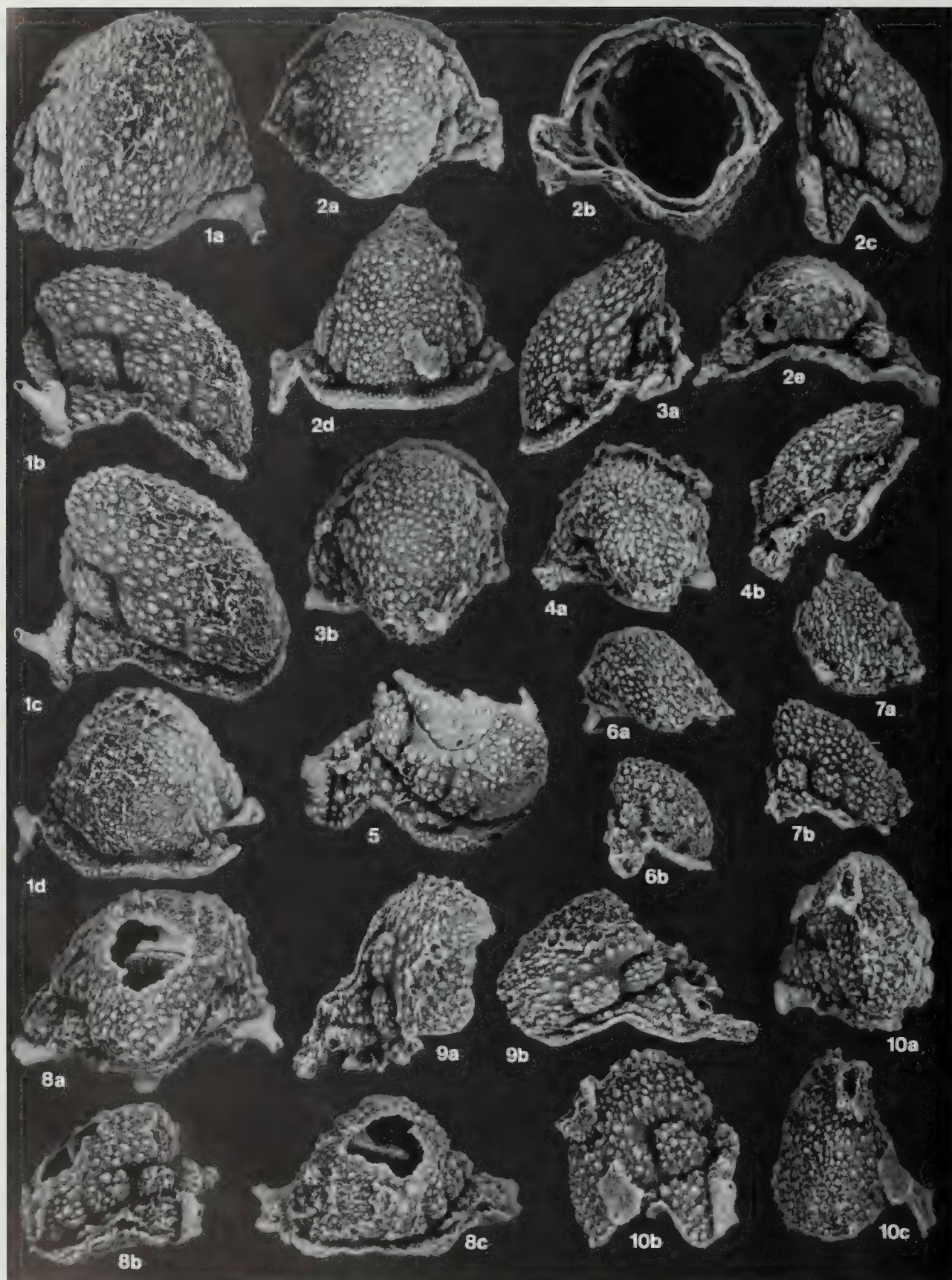


PLATE 7
Figs 1–5, 7 *Kawina divergens* (Reed, 1945). **1a–c**, It. 26019, cranidium, dorsal, anterior, and right lateral views, $\times 5$, $\times 4$, $\times 4$. **2**, SM A10396, pygidium, holotype, dorsal view, $\times 4$. **3a–b**, It. 26020, cranidium, dorsal and right lateral views, $\times 4$. **4a–b**, It. 26021, cranidium, oblique and dorsal views, $\times 4$. **5a–b**, It. 26022, cranidium, dorsal and anterior views, $\times 4$. **7a–c**, It. 26200, cranidium, dorsal, right lateral, and oblique views, $\times 7.5$.
Figs 6a–b *Mayopyge zapata* gen. et sp. nov. It. 26023, cranidium, dorsal and left dorsolateral views, $\times 15$.



Thorax unknown. Pygidium (see also Lane 1971: 56) with sagittal distance from articulating half ring furrow to rear of medial spines 44% of maximum width; pygidium composed of three distinct rings, pleural segments, and a small subtriangular terminal piece; interpleural furrows deeply incised, but first and second ribs fused to just over half distance abaxially, second and third ribs fused to about two thirds distance abaxially; pleural furrow shallow but incised on proximal part of first rib, very faint furrow visible on corresponding part of second rib; axial furrow moderately deep opposite first ring, progressively shallower posterior, but deepened around small terminal piece; first axial ring with significant sagittal convexity and bowed posteriorly in plan view; second ring less convex and more transverse; third ring not inflated and nearly transversely oriented; furrows shallowed medially; ribs with spatulate, subquadrate free tips.

DISCUSSION. *Kawina divergens* has previously been known only from its holotype pygidium (Pl. 7, fig. 2). The species is distinguished from *K. scrobiculus* (Whittington, 1963) and *K. prolificus* (Billings, 1865) in its less inflated lateral glabellar lobes and posteriorly versus anteriorly bowed occipital furrow. It differs from *K. mercurius* (Billings, 1865) in the lack of the autapomorphic transversely impressed S1 of that species. *Kawina divergens* is quite similar to both *K. griphus* and *K. torulus* (see generic discussion above), but differs from both in the presence of a much finer cephalic sculpture and an S1 that is much better impressed proximally to more fully isolate L1. The closest comparison among described species is with *K. arnoldi*. Pygidia of the two species are discussed above. Shared cephalic features include a similar sagittal convexity, similarly subdued dorsal sculpture (although that of *K. arnoldi* is slightly more robust), and similar posterior curvature of S0. The species differ particularly in the presence in *K. arnoldi* of an S1 that is strongly sigmoidal in lateral view.

Genus *MAYOPYGE* gen. nov.

TYPE SPECIES. *Mayopyge zapata* sp. nov., from the Tourmakeady Limestone, Co. Mayo, western Ireland.

OTHER SPECIES. ?*Pseudosphaerexochus tuberculatus* Warburg, 1925, Leptaena Limestones, Ashgill, Dalarne, Sweden. and the Chair of Kildare Limestone, Ashgill, eastern Ireland (Dean 1971).

ETYMOLOGY. After Co. Mayo, in which the type locality is situated, and the Greek noun *pyge*, tail.

DIAGNOSIS. Prominent eye ridge and relatively wide interocular fixigena; strong sutural ridge along anterior section of facial suture of librigena; swollen knob-like structure proximally on thoracic pleura; pygidium with three segments, anterior of which is similar to posterior thoracic segment; shallow, 'v'-shaped anterior pygidial doublural margin, with arcuate posterior embayment; densely and coarsely tuberculate dorsal sculpture.

DISCUSSION. The subfamilial affinities of *Mayopyge* gen. nov. are exceptionally difficult to judge. The densely tuberculate dorsal

exoskeleton is most similar to that developed in many acanthoparyphine clades. The prominent peak in convexity at the rear of the glabella, seen in many specimens, has obvious comparisons with the hypertrophied structure present in the same topological position in species of the primitive acanthoparyphine *Nieskowskia* Schmidt, 1881. Most species of *Nieskowskia* also have prominent tuberculate sculpture. However, *Mayopyge* lacks any of the acanthoparyphine apomorphies. Most importantly, *M. zapata* displays the primitive three-segmented pygidial condition, in contrast to the reduction to two segments characteristic of Acanthoparyphinae. In addition, the maximum glabellar width in the Irish species is achieved across L2, rather than across L1 as in acanthoparyphines.

Mayopyge does show some similarities to early species of *Sphaerexochus*. The hypostome of *M. zapata*, for example (Pl. 9, figs 17–20), is nearly identical to that of the upper Whiterockian *S. arenosus* (Chatterton & Ludvigsen, 1976, pl. 13, figs 32, 33, 37, 41, 42). *Mayopyge* also shares with *Sphaerexochus* fully isolated L1 with strong independent inflation.

In addition to several plesiomorphic features, including its relatively elongate anterior border and very prominent eye ridge, *Mayopyge zapata* displays several seemingly autapomorphic morphologies. The strong inflation of L2 and its near isolation from the median glabellar lobe in many specimens (Pl. 8, figs 1b, 2c, 9b) is not seen in any other species with a strongly inflated glabella. The thoracic pleural structure is also apparently unique. In contrast to the transverse furrow or row of pits common to most non-cheirurine cheirurids, *Mayopyge* shows only a faint, obliquely inclined furrow (Pl. 10, figs 1a, 2a, 4a), with the anterior pleural band swollen into a hemispherical knob and the posterior band greatly reduced. The structures seem analogous to those present in Cheirurinae, but in that taxon both the anterior and posterior pleural bands are swollen and the pleural furrow, though obliquely inclined, runs in a direction opposite to that seen in *Mayopyge*. In cheirurines, the pleural furrow contacts the axial furrow anteriorly, and runs posterolaterally. In *Mayopyge*, the contact is posterior and the furrow runs anterolaterally.

In summary, it does not seem possible at present to relate *Mayopyge* with confidence to other cheirurids. Potentially synapomorphic comparisons can be made with acanthoparyphines and with *Sphaerexochus*, but additional relevant diversity will probably be necessary to resolve the systematic position of the genus.

Two cranidia from the Ashgill Chair of Kildare limestone, eastern Ireland, figured by Dean (1971: pl. 11, figs 1–3, 9, 10) as *Pseudosphaerexochus? tuberculatus* Warburg, 1925, have coarse, dense, bimodal tuberculate sculpture. The species also agrees with *Mayopyge zapata* in its unusually well-impressed S2 and S3. Swedish type material of *P. tuberculatus* has never been photographically illustrated, but Warburg's (1925: pl. 10) cranidia are densely tuberculate. *Pseudosphaerexochus tuberculatus* possibly represents a species of *Mayopyge*, to which it is assigned with reservation herein, but it could equally prove to be an acanthoparyphine and confirmation will require more complete material.

Mayopyge zapata sp. nov.

Pl. 7, fig. 6; Pl. 8, figs 1–10;
Pl. 9, figs 1–21; Pl. 10, figs 1–17

PLATE 8

Figs 1–10 *Mayopyge zapata* gen. et sp. nov. **1a–d**, It. 26024, cranidium, dorsal, right lateral, oblique, and anterior views, $\times 7.5$. **2a–e**, It. 26025, cranidium, dorsal, ventral, right lateral, anterior, and posterodorsal views, $\times 10$. **3a–b**, It. 26026, cranidium, left lateral and dorsal views, $\times 10$. **4a–b**, It. 26027, cranidium, left lateral and dorsal views, $\times 10$. **5**, It. 26028, cranidium, oblique view, $\times 7.5$. **6a–b**, It. 26029, cranidium, dorsal and right lateral views, $\times 10$. **7a–b**, It. 26030, cranidium, dorsal and right lateral views, $\times 10$. **8a–c**, It. 26031, cranidium, dorsal, left lateral, and anterior views, $\times 10$. **9a–b**, It. 26032, cranidium, dorsal and oblique views, $\times 7.5$. **10a–c**, It. 26033, cranidium, dorsal, left lateral, and anterior views, $\times 10$.



ETYMOLOGY. The pygidial spines droop in the style of a moustache.

DIAGNOSIS. Occipital spine absent; L1 swollen and fully circumscribed by deep S1; S2 deep and L2 with prominent inflation; librigenal field with large, coarse pitting; first pair of pygidial spines longest.

HOLOTYPE. Pygidium It. 26059 (Pl. 10, fig. 6); paratypes It. 26023–26058, 26060–26071.

DESCRIPTION. Specimens of this taxon are so subject to varying amounts and vectors of distortion that relative cranidial dimensions are not meaningful. Anterior border relatively long (for subfamily), sculpture of numerous densely distributed fine tubercles; anterior margin with median part shaped like shallow inverted 'v' in plan view, with second distinct change in course in front of junction of axial and preglabellar furrow; anterior sections of facial sutures nearly straight, with considerable anterior convergence; axial furrows subparallel from S0 to opposite S2, anteriorly convergent in front of L2 to grade smoothly into preglabellar furrow; axial and preglabellar furrows deep; small trapezoidal frontal area with sculpture similar to anterior border; eye ridge prominent, running obliquely from opposite L3 to front of palpebral lobe, subparallel with lateral margin, defined by furrows, anterior of which is deepest, seen best ventrally (Pl. 8, fig. 2b); palpebral lobe very narrow, posteriorly contiguous with small sutural ridge; posterior furrow of eye ridge grading into incised palpebral furrow, continued posteriorly along-side posterior sutural ridge; interocular fixigena broad (tr.) for subfamily, with tuberculate sculpture somewhat coarser than that of frontal area; posterior fixigena with significant area and lateral development, subtriangular, sculpture of moderate sized tubercles; posterior border furrow similar in depth to axial furrow, of same length (exsag.) adaxially and abaxially; posterior border with strong dorsal convexity, adaxial length similar to adjoining L0, becoming longer abaxially, sculpture of fine, evenly spaced tubercles similar to that of anterior border; prominent tubular spine running posterolaterally from fulcrum of posterior border; glabella strongly inflated, prominent sculpture of fine to coarse tubercles, coarse, closely spaced tubercles becoming predominant posteriorly; sagittal convexity of most specimens showing strong peak posteriorly in cone-shaped dorsal projection in front of L0; L1 fully isolated by deep S1; L2 slightly smaller than L1; S2 well impressed, but shallower than S1; smooth band present on many specimens around anterior edge of S1 and S2; L3 strongly defined; S3 short (exsag.) and with reduced transverse course, but still quite strongly incised; S0 deep, of even length sagittally and exsagittally; L0 quite short (sag., exsag.), dorsally convex (sag., tr.), and with dense tuberculate sculpture similar to rear of pre-occipital glabella; tiny fossula present in axial furrow opposite midlength of eye ridge (Pl. 9, fig. 5b).

Librigenal lateral margin with strong, even lateral convexity; lateral border about 40% of width (tr.) of librigena, broadly inflated, with sculpture of dense tubercles, finer anteriorly and laterally, becoming coarse posteriorly along lateral border furrow; lateral

border furrow broad and deep, shallowing abruptly both posteriorly and anteriorly, terminated anteriorly by very pronounced sutural ridge along anterior section of facial suture; field with large, irregularly distributed pits and mixture of large, coarse tubercles and greater number of fine tubercles; single exsagittal row of very fine tubercles beneath eye; eye small (Pl. 9, figs 14, 16); doublure slightly narrower than lateral border, essentially flat and smooth, narrowing slightly posteriorly.

Rostral plate unknown. Hypostome with sagittal length about 55% of maximum width (excluding anterior wings) across shoulders; moderately strong sutural ridge along hypostomal suture; anterior margin anteriorly convex with more abrupt change in slope sagittally, bowed anteriorly around anterior wings; middle body separated from sutural ridge by very short (sag., exsag.) furrow, sagittal length about 60% of maximum width, sculpture of very fine tubercles, slightly coarser anteromedially; middle furrow deep laterally, running posteromedially, in some specimens shallowing but meeting sagittally to fully circumscribe anterior and posterior lobes; lateral border broad, with tuberculate sculpture slightly coarser than that of middle body; anterior wing tab-shaped, set at slightly oblique (30–45 degrees) angle; shoulder small but sharply protruded; lateral and posterior border furrows broad and very shallow; posterior border long (sag., exsag.), sculpture smooth, posterolateral corners lobate, embayed sagittally; doublure forming sharp dorsal fold and ridge around shoulder, lacking sculpture.

Thoracic segments with large articulating half-ring, set off posteriorly by sharp break in slope; axial ring longer (exsag.) laterally, shortened sagittally, sculpture of dense, fine to moderate sized tubercles; axial ring separated from articulating half-ring by broad, long preannular lobe, always developed as a depressed area, never with independent inflation; axial furrow very shallow, ring nearly contiguous with pleura; pleura proximal to fulcrum composed of subrectangular base topped by semicylindrical rib; rib with prominent knob-like swelling on anteroproximal part, with shallow, oblique furrow set posterior to swelling (Pl. 10, fig. 4a); pleura distal to fulcrum composed of free, tubular spine, lengthening and more posteriorly inclined on more posterior segments, with dorsal sculpture of moderately sized tubercles.

Pygidium composed of three segments, anterior segment with morphology essentially identical to that of posterior thoracic segment; articulating half-ring separated from first axial ring by narrow furrow, preannular lobe absent; axial furrows subparallel and deep on first segment, very shallow on second, entirely effaced on third; first axial ring with robust tuberculate sculpture; second ring very short (sag., exsag.), with four or five tubercles of same size as those on first ring; ring furrow between first and second rings broad and deep, forming pit laterally; second ring furrow slot-like (Pl. 10, figs 11a, 14a), in many specimens reduced to lateral pits (Pl. 10, figs 7, 9); third segment expressed as pair of median spines united by small, tuberculate terminal piece; first spine pair elongate, posteriorly recurved; second and third pairs progressively shorter; all spines with dorsal and dorsolateral tuberculate sculpture similar in size and

PLATE 9

Figs 1–21 *Mayopyge zapata* gen. et sp. nov. **1.** It. 26034, cranidium, dorsal view, $\times 6$. **2.** It. 26035, cranidial fragment, dorsal view, $\times 10$. **3a–b.** It. 26036, cranidium, dorsal and left lateral views, $\times 7.5$. **4.** It. 26037, cranidium, dorsal view, $\times 7.5$. **5a–c.** It. 26038, cranidium, dorsal, ventral, and anterior views, $\times 10$. **6a–c.** It. 26039, cranidium, left lateral, dorsal, and anterior views, $\times 10$. **7a–b.** It. 26040, cranidium, dorsal and left lateral views, $\times 7.5$. **8.** It. 26041, cranidium, dorsal view, $\times 7.5$. **9a–b.** It. 26042, right librigena, external and internal views, $\times 10$. **10.** It. 26043, left librigena, external view, $\times 7.5$. **11.** It. 26044, right librigena, external view, $\times 7.5$. **12.** It. 26045, right librigena, external view, $\times 10$. **13.** It. 26046, left librigena, external view, $\times 7.5$. **14.** It. 26047, left librigena, external view, $\times 10$. **15.** It. 26048, right librigena, external view, $\times 7.5$. **16.** It. 26052, right librigena, external view, $\times 7.5$. **17a–b.** It. 26049, hypostome, ventral and dorsal views, $\times 7.5$. **18.** It. 26050, hypostome, ventral view, $\times 10$. **19.** It. 26051, hypostome, ventral view, $\times 7.5$. **20.** It. 26053, hypostome, ventral view, $\times 7.5$. **21a–b.** It. 26054, cranidium, oblique and posterior views, $\times 7.5$.



density to that of first axial ring; doublure forming narrow, convex ventral rim, with fine tuberculate sculpture; anterior doublural margin 'v'-shaped, with median posterior embayment.

DISCUSSION. This species is the second most common in our collections and, like other common taxa, displays several morphotypes due to tectonic distortion. In *Mayopyge zapata* the distortion seems to be nearly bimodal. Overwhelmingly common among the cranidia is the type illustrated on Pl. 8, which displays a conical dorsal swelling of the glabella in front of the occipital ring. Whether this is a biological structure or a the result of distortion and enhancement of an original convexity peak is not known. The structure is so pervasive that it seems likely that at least some original inflation was present. The second cranidial type is that illustrated on Pl. 9, figs 1, 3a, 4, 5a, in which this projection is entirely absent and the glabella roundly and evenly inflated. An undistorted calcareous crackout cranidium (Pl. 7, fig. 6) shows an inflated convexity peak at the rear of the glabella. It is conceivable that different vectors and amounts of distortion could produce either of the silicified morphotypes from such an original morphology.

Pygidial types do not show as strong a disjunct occurrence as do the cranidia, but are even more morphologically discrete. The slightly more common form (Pl. 10, figs 6–10, 12, 13, 17) includes the holotype. It is relatively long versus wide (sagittal length 45–50% of anterior width), has long, posteriorly directed spines, a second ring furrow that is typically reduced to two lateral pits, and a rather sharp doublural embayment (Pl. 10, figs 6b, 8b). The second, slightly less common, form (Pl. 10, figs 11, 14–16) is much shorter (sagittal length 27–33% of anterior width), has more laterally splayed spines, with the median pairs apparently shorter, a second ring furrow that is a medially continuous slot (Pl. 10, figs 11a, 14a, 15a), and a relatively shallow doublural embayment (Pl. 10, figs 11b, 15b).

Given the apparent presence of two cranidial and pygidial morphotypes, there are three possibilities. First, the variation may be genuine and reflect sexual dimorphism. Second, the variation may be genuine and reflect the presence of two closely related species. And third, the dimorphism may be artefactual, and a result of the tectonic distortion affecting the entire fauna. Sexual dimorphism is improbable; it remains unproven in the trilobites as a whole (Adrain & Kloc 1997; Hughes & Fortey 1996; Ramsköld & Chatterton 1991; Ramsköld & Werdelin 1991). If sexual dimorphism were the case it might be expected that other acathoparyphines would also exhibit it, which species known from abundant silicified material manifestly do not. It cannot be entirely disproved that there are two, closely related species: since cheirurid pygidia are distinctive the name is attached to the best specimen of the commonest morph. Overall, we consider that bimodal tectonic distortion is responsible for the variation, since 'long' and 'short' forms have also been recognised in *Iliaenus weaveri* and *Celmus michaelmus*, where the cause is demonstrably tectonic. However, the pygidial differences remain a cause for concern, as the different ring furrows are not readily accounted for by distortion alone.

Subfamily **CHEIRURINAE** Hawle & Corda, 1847

Genus **CERAURINELLA** Cooper, 1953

TYPE SPECIES. *Ceraurinella typa* Cooper, 1953, from the Edinburg Formation (Mohawkian), Virginia, U.S.A.; by original designation.

Ceraurinella sp.

Pl. 11, figs 1–9

MATERIAL. Assigned specimens It. 26072–26080.

DISCUSSION. The fragmentary nature of the available material does not allow a determination of the species, and several important morphological differentia (e.g., eye position) are not fully preserved. Nevertheless, the Tourmakeady species is clearly a primitive member of the *Ceraurinella* group (including *Sycophantia* Fortey, 1980). The Irish species differs from the Spitsbergen plesiomorph *S. seminosa* Fortey, 1980, in its much shorter anterior cranidial border (in which it resembles later and presumably more advanced species) and in the complete loss of the small median pygidial spine retained in *S. seminosa*. Both the available librigenae and fixigenal fragments, however, indicate that the Irish species retained very wide posterior fixigenae, similar to *S. seminosa*. Of other early species, the Tourmakeady taxon resembles *C. polydorus* (Billings, 1865) (see Whittington 1965: pl. 60) in the length of the anterior cranidial border, but differs in possessing less inflated lateral glabellar lobes (compare Pl. 11, fig. 1 with Whittington 1965: pl. 60, fig. 4), a broader posterior fixigena, and a narrower pygidium lacking an independently defined median spine.

Family **ENCRINURIDAE** Angelin, 1854

Subfamily **CYBELINAE** Holliday, 1942

Cybeline indet. (not figured)

MATERIAL. Assigned specimen It. 26201.

DISCUSSION. A single very poorly preserved cybeline cranidium has been recovered from the silicified residues. It is obscured by silicified debris, and identifiable only to subfamily level. It is noted here for completeness.

Family **LECANOPYGIDAE** Lochman, 1953

Genus **BENTHAMASPIS** Poulsen, 1946

TYPE SPECIES. *Benthamaspis problematica* Poulsen, 1946, Ibexian, Ellesmere Island, Canadian Arctic; by monotypy.

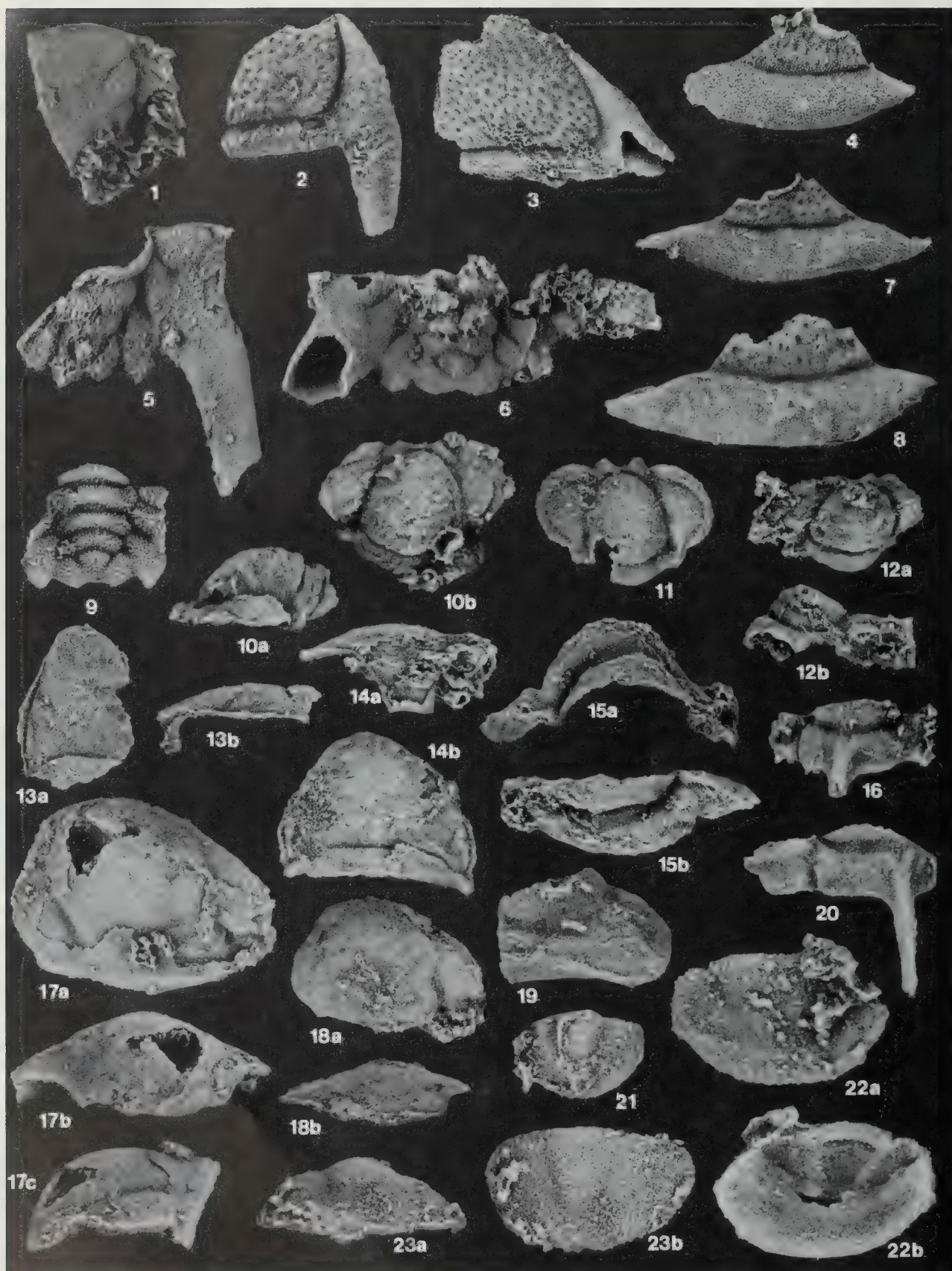
Benthamaspis aff. *B. diminutiva* Hintze, 1953

Pl. 11, figs 17–19, 21–23

MATERIAL. Assigned specimens It. 26089–26094.

PLATE 10

Figs 1–17 *Mayopyge zapata* gen. et sp. nov. **1a–b**, It. 26055, thoracic segment, dorsal and anterior views, $\times 7.5$. **2a–b**, It. 26056, thoracic segment, dorsal and anterior views, $\times 7.5$. **3a–b**, It. 26057, thoracic segment, dorsal and anterior views, $\times 7.5$. **4a–b**, It. 26058, thoracic segment, dorsal and anterior views, $\times 7.5$. **5a–b**, It. 26060, thoracic segment, oblique and dorsal views, $\times 7.5$. **6a–c**, It. 26059, holotype, pygidium, right lateral, dorsal, and ventral views, $\times 7.5$. **7**, It. 26061, pygidium, dorsal view, $\times 10$. **8a–b**, It. 26064, pygidium, dorsal and ventral views, $\times 7.5$. **9**, It. 26062, pygidium, dorsal view, $\times 7.5$. **10**, It. 26063, pygidium, dorsal view, $\times 10$. **11a–b**, It. 26066, pygidium, dorsal and ventral views, $\times 7.5$. **12**, It. 26065, pygidium, dorsal view, $\times 10$. **13**, It. 26067, pygidium, dorsal view, $\times 10$. **14a–b**, It. 26068, pygidium, dorsal and posterior views, $\times 7.5$. **15a–b**, It. 26069, pygidium, dorsal and ventral views, $\times 7.5$. **16**, It. 26070, pygidium, dorsal view, $\times 7.5$. **17**, It. 26071, pygidium, dorsal view, $\times 10$.



DISCUSSION. Fortey (1979: 100) has discussed the evolutionary trends evident in *Benthamaspis*, culminating in the considerably effaced species *B. diminutiva* Hintze, 1953. A species from the Tourmakeady Limestone is of interest in that it is the youngest known member of the genus and confirms the stratigraphically correlated pattern of progressive effacement. The species is very similar to the slightly older (Zone J) *B. diminutiva*, from Ibex, Utah, but differs in the possession of narrower palpebral lobes, more well impressed axial furrows, and retention of a complete, if very shallow, preglabellar furrow. The preglabellar furrow of *B. diminutiva* is effaced, so that the glabella grades anteriorly toward the anterior border furrow (Hintze 1953: pl. 13, figs 9b, 10c). In addition to effacement, the species are united by their nearly identical pygidia (compare Pl. 11, fig. 23, with Hintze 1953: pl. 13, figs 11a, 11b), and by the laterally concave glabellar margins. Most older Ibexian species have the axial furrows anteriorly convergent, but there is some indication of the beginnings of the axially bowed form with an anteriorly expanding glabella in certain specimens of *B. conica* Fortey, 1979, from the Catoche Formation of western Newfoundland (see particularly Fortey 1979: pl. 35, fig. 7). The librigena of *B. diminutiva* is not known, but that of the Irish taxon (Pl. 11, fig. 19) agrees well with those assigned to earlier species (Fortey 1979: pl. 34, fig. 3; pl. 35, fig. 4). We also figure as *Benthamaspis* sp. two cranidia with distinct borders (It 25941, 25942; Pl. 1, figs 7, 9) which are probably not conspecific with *B. aff. diminutiva*; a pygidium (It 25943; Pl. 1, fig. 8) may belong with these cranidia.

Family **TELEPHINIDAE** Marek, 1952
Subfamily **TELEPHININAE** Marek, 1952
Genus **OOPSITES** Fortey, 1975a

TYPE SPECIES. *Telephus hibernicus* Reed in Gardiner & Reynolds, 1909, from the Tourmakeady Limestone, upper Arenig, Ireland; by original designation.

DISCUSSION. *Oopsites* was erected (Fortey 1975a: 95) as an explicit 'morphological and stratigraphic intermediate' between the genera *Goniophrys* Ross, 1951, and *Telephina* Marek, 1952. As such, it may well prove paraphyletic. The situation, however, would be better understood in light of a comprehensive phylogenetic review of the telephinids, a task beyond the scope of the present work, and the original classification is retained herein.

Oopsites hibernicus (Reed in Gardiner & Reynolds, 1909)
Pl. 11, figs 10–12, 15; Pl. 13, figs 1–3; Pl. 16, fig. 24

1909 *Telephus hibernicus* Reed in Gardiner & Reynolds: 149; pl. 6, figs 10, 11.

1930 *Telephus hibernicus* Reed; Ulrich: 17; pl. 2, figs 18, 19.

1968 *Telephina hibernica* (Reed); Whittington: 56.

PLATE 11

Figs 1–9 *Ceraurinella* sp. 1. It. 26072, cranidium, dorsal view, $\times 8$. 2. It. 26073, cranidial fragment, dorsal view, $\times 6.5$. 3. It. 26074, cranidial fragment, dorsal view, $\times 6.5$. 4. It. 26075, right librigena, external view, $\times 10$. 5. It. 26076, pygidium, dorsal view, $\times 8$. 6. It. 26077, pygidium, dorsal view, $\times 6.5$. 7. It. 26078, left librigena, external view, $\times 10$. 8. It. 26079, right librigena, external view, $\times 3.5$. 9. It. 26080, pygidium, dorsal view, $\times 10$.

Figs 10–12, 15 *Oopsites hibernicus* (Reed in Gardiner & Reynolds, 1909). **10a–b**, It. 26081, cranidium, left lateral and dorsal views, $\times 10$. **11**, It. 26082, cranidium, dorsal view, $\times 15$. **12a–b**, It. 26083, cranidium, dorsal and anterior views, $\times 10$. **15a–b**, It. 26086, thoracic segment, anterior and dorsal views, $\times 7.5$.

Figs 13, 14, 16, 20 *Opipeuter* aff. *O. inconnivus* Fortey, 1974 **13a–b**, It. 26108, cranidium, dorsal and left lateral views, $\times 10$. **14a–b**, It. 26109, cranidium, anterior view, $\times 10$. **16**, It. 26087, thoracic segment, dorsal view, $\times 15$. **20**, It. 26088, thoracic segment, dorsal view, $\times 10$.

Figs 17–19, 21–23 *Benthamaspis* aff. *B. diminutiva* Hintze, 1953 **17a–c**, It. 26089, cranidium, dorsal, anterior, and left lateral views, $\times 10$. **18a–b**, It. 26090, cranidium, dorsal and anterior views, $\times 10$. **19**, It. 26091, left librigena, external view, $\times 10$. **21**, It. 26092, pygidium, dorsal view, $\times 15$. **22a–b**, It. 26093, pygidium, dorsal and ventral views, $\times 15$. **23a–b**, It. 26094, pygidium, posterior and dorsal views, $\times 15$.

1975a *Oopsites hibernicus* (Reed); Fortey: 97; pl. 33, figs 9–19; pl. 34, figs 1–7.

1988 *Oopsites hibernicus* (Reed); Morris: 156.

MATERIAL. Topotypes It. 26081–26083, 26086–26088, 26111–26113, 26176.

DISCUSSION. Fortey (1975a: 97, pl. 33, fig. 8) designated and illustrated a lectotype from Reed's (in Gardiner & Reynolds 1909) syntypes. This has been the only photographic illustration of a type specimen to date, although Fortey (1975a) figured well preserved Spitsbergen material assigned to the species. The additional Irish material figured herein confirms the specific identity with the Spitsbergen taxon beyond any doubt. The only possible difference between the two lots of specimens is that the palpebral furrow of the Spitsbergen cranidia is slightly deeper anteriorly than that of the Irish specimens (compare Fortey 1975a: pl. 33, fig. 12; pl. 34, fig. 6, with Pl. 13, fig. 1b).

Subfamily **OPIPEUTERINAE** Fortey, 1974

DISCUSSION. Opipeuteridae was originally proposed as a monogeneric family by Fortey (1974), who considered that this specialised pelagic form might be closest to remopleuridoids. Shergold (in Laurie & Shergold 1996) demonstrated that it is instead closely related to *Carolinites*, and hence a member of the Telephinidae. It is not yet clear how the *Carolinites* + *Opipeuter* group, which is very likely monophyletic, relates to other telephinids. Dean (1971) introduced the subfamily Carrickiinae to accommodate *Carrickia*, and the relationship of this genus to *Telephina* and *Goniophrys*, and all of these to *Carolinites* and *Opipeuter*, is as yet unclear. For the time being Opipeuterinae is retained as a subfamily of telephinids, to include *Opipeuter* and *Carolinites*, pending the clarification of their relationships to other pelagic taxa.

Genus **OPIPEUTER** Fortey, 1974

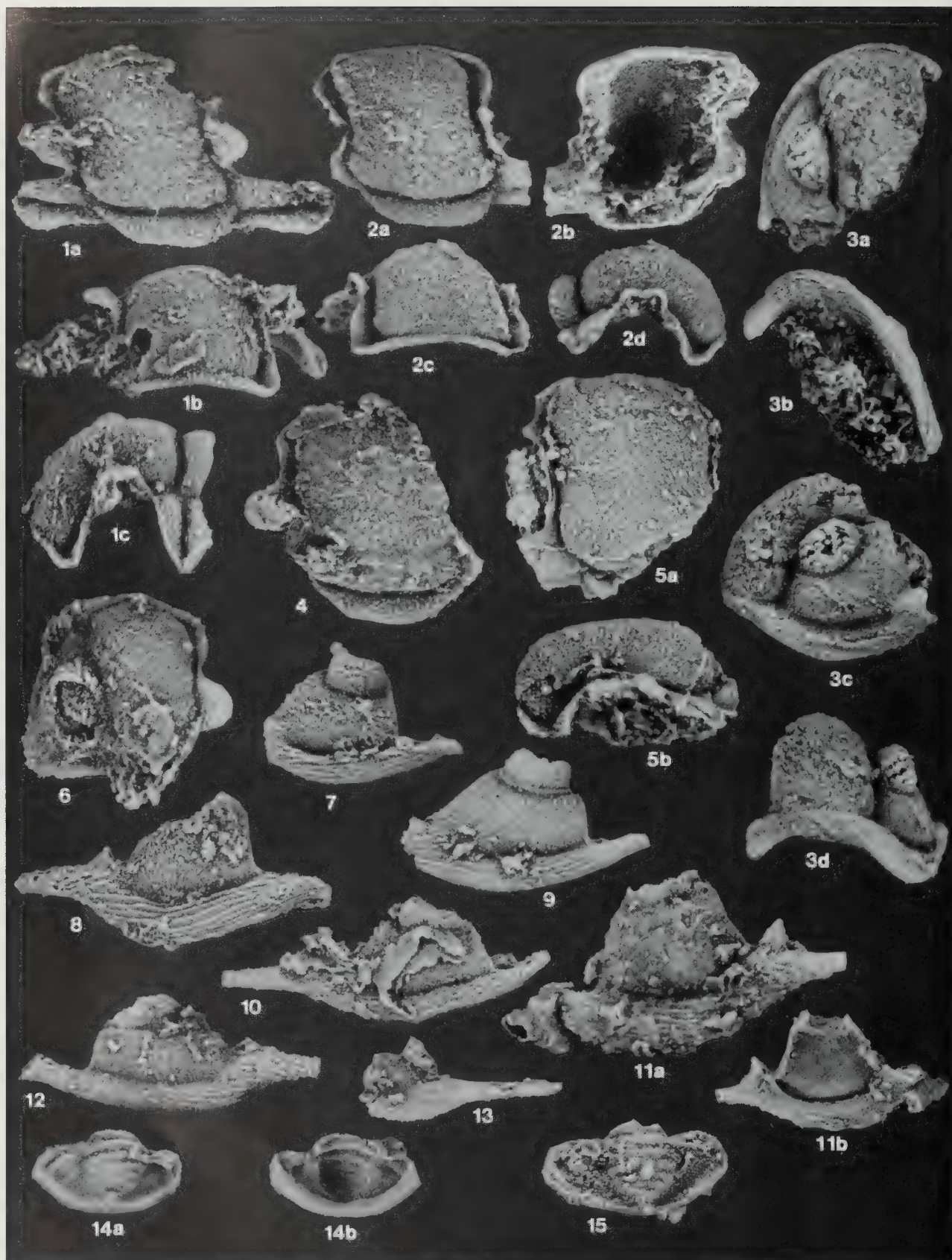
TYPE SPECIES. *Opipeuter inconnivus* Fortey, 1974, from the Valhallfonna Formation (Arenig) of Spitsbergen; by original designation.

Opipeuter aff. *inconnivus* Fortey, 1974

Pl. 11, figs 13, 14, 16, 20; Pl. 13, figs 4, 5

MATERIAL. Assigned specimens It. 26087, 26088, 26108, 26109, 26114, 26115.

DISCUSSION. *Opipeuter inconnivus* was fully described by Fortey (1974) who included within that species a cranidium from the Tourmakeady Limestone. There are three species in stratigraphical succession through the Arenig, each with progressively narrower anterior glabellar tongues: *O. angularis* (Young, 1973), *O. inconnivus*, and *Opipeuter*. sp. A of Fortey (1974), the last-named also having a



relatively wide genal field. New silicified material (Pl. 11, fig. 14a) shows a slightly narrower (tr.) glabellar tongue than is typical of *O. inconnivus*, and the librigena (Fortey 1974, pl. 14, fig. 13) has a relatively wide genal field. The population seems to be intermediate between *O. inconnivus* and *Opipeuter* sp. A, and it is considered preferable to term it *O. aff. inconnivus*. Henderson (1983) described *O. insignis* from Queensland, Australia, based upon rather fragmentary material. The genal field is like that of *O. aff. O. inconnivus*. Henderson also stated that one thoracic segment carried a long, median spine. Fortey's (1974) reconstruction of *O. inconnivus* did not show such a spine, but was based upon an entire specimen in which the thoracic axis was poorly preserved. It seems likely that the thoracic segments figured here on Pl. 11, figs 16, 20 are this spinose segment.

Family LEIOSTEGIIDAE Bradley, 1925

Genus *AGERINA* Tjernvik, 1956

TYPE SPECIES. *Agerina erratica* Tjernvik, 1956, from the 'grey marly Upper Planilimbata limestone,' Lanne, Närke, Sweden; by original designation.

Agerina palabunda sp. nov.

Pl. 12, figs 1–15

ETYMOLOGY. Latin, wandering, referring to the widespread occurrence of the genus.

HOLOTYPE. Cranium, It. 26095 (Pl. 12, fig. 1); paratypes It. 26096–26107, 26084, 26085.

DIAGNOSIS. Glabellar furrows almost entirely effaced, except for smooth patch at S1; glabella with clavate form, axial furrows strongly bowed inwards; dorsal cephalic sculpture of fine tubercles.

DESCRIPTION. Cranium with sagittal length about 60% of maximum width across posterior border furrows; width across midlength (exsag.) of palpebral lobes two thirds that across posterior border furrows; anterior sections of facial sutures strongly divergent anteriorly in front of palpebral lobes, reaching maximum divergence opposite anterior border furrow, then strongly convergent opposite anterior border; posterior sections of facial sutures curving sharply immediately behind palpebral lobe to run nearly transversely, curving posteriorly around distal extremity of posterior fixigena; anterior border short (sag., exsag.), upturned, nearly flat, almost completely overhung by glabella medially, with sculpture of two or three linear terrace lines running parallel to margin; border lengthening abaxially, separated from anterior fixigena by weakly impressed border furrow; glabella moderately inflated, hourglass-shaped, anterior margin with gentle anterior convexity, lateral margins with strong lateral concavity; glabellar sculpture of dense, evenly distributed fine tubercles, all of similar size; S1 not incised, reflected as a smooth patch free of tuberculate sculpture (Pl. 12, figs 4, 5); anterior glabellar furrows indiscernible; anterior fixigena confined to narrow, subtriangular strip; axial furrow very deeply incised, bowed

strongly adaxially beside palpebral lobe; palpebral lobe large, similar in length (exsag.) to posterolateral projection of cranium, held in horizontal plane, with dorsal sculpture of dense granules; posterior fixigena forming relatively long (exsag.) transverse strip, sculpture of fine tubercles similar to that of glabella; posterior border furrow similar in depth to axial furrow, of similar length medially and laterally, running nearly exactly transversely; posterior border relatively short proximally, lengthening and becoming slightly lobate laterally, with considerable exsagittal dorsal convexity; S0 with gentle posterior curvature, similar in depth and incision to axial furrow and posterior border furrow; L0 with posterior margin describing very shallow 'W' shape so that sagittal length is slightly shorter than nearby exsagittal length, then shortening considerably behind L1; L0 with tuberculate sculpture similar to that of anterior part of glabella, no distinct median node discernible, with moderate sagittal convexity.

Librigenal field with anterior width (tr.) 60–65% of maximum width just behind eye; maximum width about 55% of maximum length (exsag.); lateral border broad, slightly wider posteriorly than anteriorly, with prominent, rounded, dorsal inflation, sculpture of about nine coarse terrace lines, arranged subparallel to lateral margin anteriorly, running back to intersect margin posteriorly, more closely spaced near lateral margin, slightly anastomosing with some merging and disappearance of individual lines; lateral border furrow deep, narrow, shallowing abruptly posteriorly in front of genal spine; lateral border furrow and lateral margin with strong lateral curvature; genal spine long and tapering, terrace lines of lateral border continued along length without interruption; only small portion of posterior border developed on librigena, beside strong sutural embayment for posterolateral part of cranium; field with gentle dorsal convexity, sculpture of fine tubercles, slightly coarser adaxially and beneath eye; prominent eye socle of single continuous, narrow band; eye large, with length (exsag.) slightly more than double width at midlength; doublure nearly flat, with subdued terrace lines developed mainly near lateral margin, much finer than those on dorsal aspect of lateral border.

Rostral plate subrectangular in anterior aspect, connective sutures longer than rostral suture; terrace lines of anterior librigenal projections continued across plate without interruption; connective sutures converging ventrally, nearly meeting posteriorly on strongly curved ventral part of plate.

Thorax unknown. Pygidium with sagittal length 50–55% of maximum width; wide, gently tapering and obtusely rounded axis slightly less than half pygidial width (as shown on best silicified specimen, Pl. 12, fig. 14a); axis extends close to border, in contact via narrow postaxial ridge; five narrow (tr.) axial rings extending to postaxial ridge; posteriormost ring may be obscure; gently convex pleural fields show two defined segments, only the anterior pleural furrows are at all deep; border is narrow and distinctly convex, and carries a sculpture of a few raised lines like those on the genal border; doublure recurved ventrally and wider than border, showing an anterolateral articulatory 'tooth' (cf. *Annamitella* Fortey & Shergold 1984, pl. 38, fig. 15).

PLATE 12

Figs 1–15 *Agerina palabunda* sp. nov. **1a–c**, It. 26095, **holotype**, cranium, dorsal, anterior, and left lateral views, $\times 15$. **2a–d**, It. 26096, cranium, dorsal, ventral, anterior, and right lateral views, $\times 15$. **3a–d**, It. 26097, cephalon, dorsal, ventral, left lateral, and anterior views, $\times 15$. **4**, It. 26098, cranium, dorsal view, $\times 15$. **5a–b**, It. 26099, cranium, dorsal and left lateral views, $\times 15$. **6**, It. 26100, cranium and left librigena, dorsal view, $\times 15$. **7**, It. 26101, right librigena, external view, $\times 15$. **8**, It. 26102, right librigena, external view, $\times 15$. **9**, It. 26103, right librigena, external view, $\times 15$. **10**, It. 26104, right librigena, external view, $\times 15$. **11a–b**, It. 26107, left librigena, external and internal views, $\times 15$ and $\times 10$. **12**, It. 26105, left librigena, external view, $\times 15$. **13**, It. 26106, left librigena, external view, $\times 15$. **14a–b**, It. 26084, pygidium, dorsal and ventral views, $\times 10$. **15**, It. 26085, pygidium, dorsal view, $\times 10$.

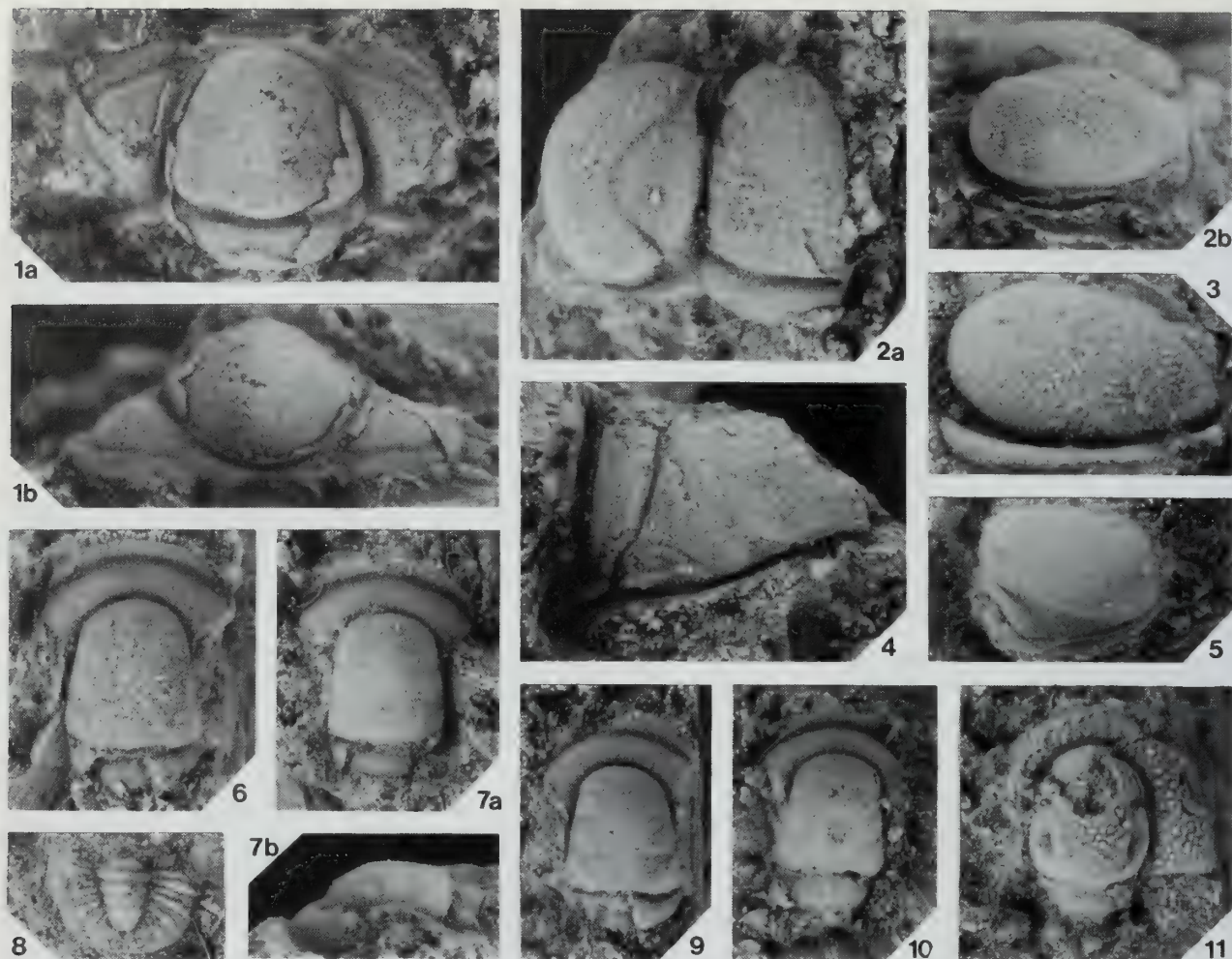


PLATE 13

- Figs 1-3** *Oopsites hibernicus* (Reed in Gardiner and Reynolds, 1909). **1a-b**, It. 26111, cranidium, dorsal and anterior views, $\times 15$. **2a-b**, It. 26112, cranidium and left librigena, dorsal and left lateral views, $\times 15$. **3**, It. 26113, left librigena, left lateral view, $\times 15$.
- Figs 4, 5** *Opipeuter* aff. *O. incommisus* Fortey, 1974 **4**, It. 26114, cranidium, right dorsolateral view, $\times 15$. **5**, It. 26115, right librigena, external view, $\times 15$.
- Figs 6, 7, 9, 10** *Phaseolops ceryx* sp. nov. **6**, It. 12856, cranidium, dorsal view, $\times 15$. **7a-b**, It. 12857, cranidium, dorsal and left lateral views, $\times 15$. **9**, It. 26116, cranidium, dorsal view, $\times 15$; **10**, It. 26117, cranidium, dorsal view, $\times 15$.
- Fig. 8** *Proscharyia platylimbata* sp. nov. It. 26118, pygidium, dorsal view, $\times 15$.
- Fig. 11** *Glaphurus crinitus* sp. nov. It. 26119, cranidium, dorsal view, $\times 10$.

DISCUSSION. Ludvigsen (1980: 99) has fully discussed this genus, assigning it to the Bathyruridae. Fortey & Shergold (1984: 322) considered that it was related to *Annamitella* Mansuy, 1920, on the basis of glabellar characters, and assigned both to Leiostegiidae. Within the genus as conceived by these workers there is a group of similar species, including *A. acheila* (Harrington & Leanza, 1957), *A. norrisi* Ludvigsen, 1980, and *A. praematura* Tjernvik, 1956. It is these species that most resemble *Annamitella*, and all have a relatively elongate anterior border, incised glabellar furrows, a concave-sided glabella, and a pygidium with a subdued border lacking raised lines. The Sunwaptan species described as *Bellaspidea parallela* Ludvigsen & Westrop in Ludvigsen *et al.* 1989, appears to share all of these morphological features, and may prove to belong there. All are seemingly related to the Chinese taxon *Hexianella* Zhang, 1983, to which they are transferred herein. The pygidia assigned to *H. hexianensis* and *H. exigulcata* by Zhang

(1983: pl. 75, figs 6, 8) do not belong, but appear to be nileid transitory pygidia.

A second group includes the type species of *Agerina* and *A. pamphylica* Dean, 1973. These species have the glabellar furrows considerably effaced, the glabella more nearly parallel sided, and the pygidium with a border carrying prominent subparallel raised lines. Of described species, *A. palabunda* is closer to this second, Arenig, group, and is perhaps most similar to *A. pamphylica*. Dean's species does show some lateral concavity of the glabella (Dean 1973: pl. 4, fig. 1), although it is less well developed and anterior than in *A. palabunda*.

Family **CELMIDAE** Jaanusson, 1956
Genus **CELMUS** Angelin, 1854

Ischyrophyma Whittington, 1963: 48.

TYPE SPECIES. *Celmus granulatus* Angelin, 1854, Skarpasen, Östergötland, Sweden; by monotypy.

OTHER SPECIES. *Glaphurina? insolita* Tjernvik, 1956; *Celmus? longifrons* Poulsen, 1965; *Ischyrophyma tuberculata* Whittington, 1963; *Ischyrophyma tumida* Whittington, 1965; *Ischyrophyma? sp. indet.* of Whittington (1963); the specimen figured by Whittington (1965: pl. 19, figs 16, 19, 20) as *Ischyrophyma? sp. indet.* is a calymenid related to or conspecific with his 'aff. *Calymenidius sp. ind.*' (Whittington 1965: pl. 59, figs 10, 12–15); work in progress on silicified Newfoundland faunas indicate this taxon is a species of *Sthenarocalymene* Siveter, 1977.

***Celmus michaelmus* sp. nov.**

Pl. 14, figs 1–17; Pl. 15, figs 1, 2, 5–9; Pl. 16, figs 11, 20

1975 *Celmus* sp. Fortey & Owens Fig. 1A,B

ETYMOLOGY. Latin, a mouse called Michael (see Pl. 15, fig. 6a).

DIAGNOSIS. Dorsal sculpture densely tuberculate; several exsagittal rows of tubercles on anterior fixigena; posterolateral part of librigenal lateral border with sparse or absent tubercles, but prominent raised lines subparallel with margin; pygidium with nearly elliptical outline in plan view; pygidial flanges circular and prominent.

HOLOTYPE. Pygidium, It. 26123 (Pl. 14, fig. 4); paratypes It. 12853, 12854, 26120–26122, 26124–26141, 26168, 26169.

DESCRIPTION. Some of the silicified material upon which this species is based has suffered distortion; for example, the original of Pl. 14, fig. 6 has been foreshortened, and that of Pl. 14, fig. 3, elongated sagittally. The holotype, and such specimens as that figured on Pl. 14, fig. 2, are considered close to the undistorted state, and it is upon these that descriptions of proportions are based.

Cranidium as wide (tr.) at the posterior margin as long (sag.), this being three-quarters the width across the palpebral lobes; glabella about 1.5 times longer than wide, the maximum width being at L1 where the glabella bulges outwards before tapering gently anteriorly; S1 deep and distinct, the outer part slightly wider and almost transverse, the inner part geniculated backwards and on most specimens just falling short of reaching the occipital furrow (Pl. 14, fig. 7, in which it does, is also distorted); S2 is short, transverse, close to the anterior end of the palpebral lobe; glabella encroaches on the border, but at least some part of the border is visible in dorsal view; fixigenal and eye position are as in all other species of the genus; the palpebral lobes carry three or four prominent tubercles.

Librigena retains a knob at the genal angle, which is a remnant genal spine; on a small example (Pl. 14, fig. 12) it is much more prominent; bevelled border bears three or four very prominent raised lines which extend as far as the knob; a few scattered tubercles may be present between the lines; the elevated eye has a smooth eye socle beneath it, at its anterior end, a small, inflated lobe (see Pl. 15, fig. 1); doublure extends beneath border (Pl. 14, fig. 17), and carries an exterior groove on its posterolateral edge, which may have accommodated pleural tips upon enrollment (see Bruton 1983, pl. 28, fig. 2).

Thoracic segment shows general convexity of body (Pl. 15, fig. 2b); anterior ridge terminates in an articulatory notch; posterior band continues distally as a spine.

Minute pygidium is known from good isolated material; it comprises a single segment, with an articulating half-ring; posterior margin densely covered with raised lines subparallel to margin, and narrow doublure (Pl. 15, fig. 6c) with fine terrace lines; pygidium bears a pair of flat, rounded flanges which project backwards; the surface of the flanges is smooth.

The rest of the axial part of the exoskeleton, and the genal fields, is densely tuberculate; in some specimens the librigenal tubercles are of two sizes (Pl. 15, fig. 1), but this is less clearly so in others (Pl. 14, fig. 11).

DISCUSSION. This species is very similar indeed to the type species, *Celmus granulatus* (see Jaanusson 1956, Bruton 1983) from the Kundan stage of Sweden. Cephalic differences are trivial. The distinctive lobe at the anterior end of the eye socle of *C. michaelmus* is not mentioned in a detailed description by Bruton (1983, p. 216), but is visible on his figures (*ibid.*, pl. 28, fig. 14). The sculpture on the Irish species is denser; for example the anterior fixed cheek of *C. granulatus* shows a single row of tubercles except at the anteriormost end, while several rows are present along its whole length in the new species (Pl. 14, figs 1c, 2c, 6b). The raised lines which extend to the genal spine remnant on the librigenal border of *C. michaelmus* stop well short of it in *C. granulatus*, and the portion of the border in front of the genal angle is far more densely tuberculate in the latter species. Finally, the prominent pygidial flanges of the Tourmakeady species are much better developed than a homologous pair of low ridges in *C. granulatus* (Bruton 1983: pl. 28, figs 10, 12), and the pygidium of the Irish species has an elliptical, versus trapezoidal, outline in plan view.

Genus ***DIMEROPYGE*** Öpik, 1937

TYPE SPECIES. *Sphaerexochus minutus* Nieszkowski, 1857, Middle Ordovician, Kukruse beds, Estonia; by monotypy.

***Dimeropyge? ericina* sp. nov.**

Pl. 15, figs 15–17; Pl. 16, figs 17–19, 21–23

ETYMOLOGY. Latin, of a hedgehog.

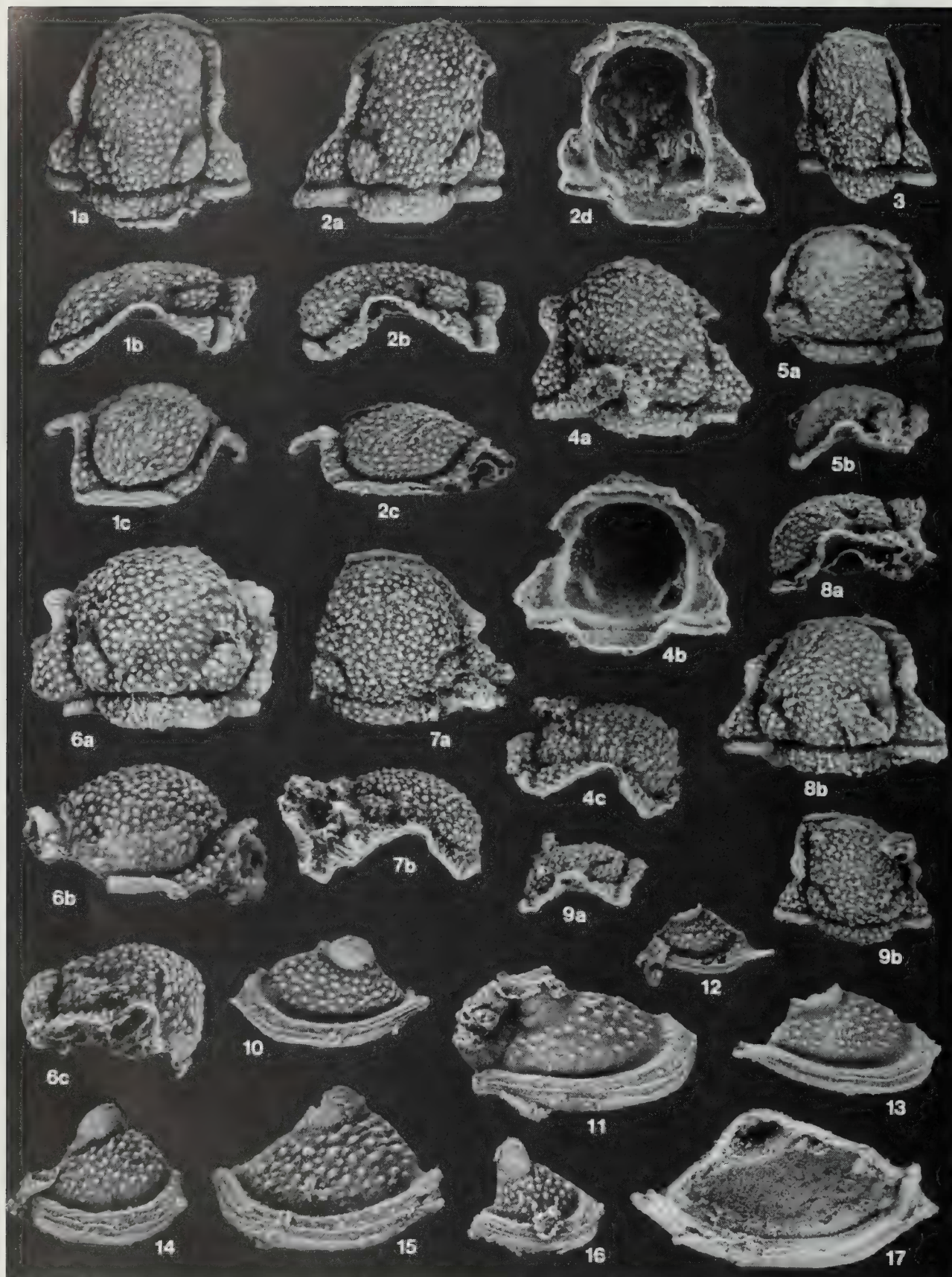
DIAGNOSIS. Elongate glabellar spines retained in holaspis; two pairs of glabellar spines, four pairs of fixigenal spines; librigena carries two spines on genal field and a few on border.

HOLOTYPE. Cranidium, It. 26150 (Pl. 15, fig. 15); paratypes It. 26151, 26152, 26170–26175.

DESCRIPTION. We have not discovered a pygidium of this unusual species, but the cephalic parts are so distinctive that it can be named as new.

Glabellar outline is best seen on the inner surface of the cranidium (Pl. 15, fig. 15b), which shows it extending to two-thirds cephalic length, convex (tr.), defined by deep axial furrows; width at L0 wider (tr.) than in front, thereafter expanding gently in width anteriorly to rounded front; L0 carries a pair of long, stout spines; two equally stout pairs are present on the glabella; fixigena are wider than glabella at posterior margin; they, too, carry spines, which can be matched with the glabellar ones, since one pair on the rather poorly defined posterior border matches the occipital segment, and there are two pairs anterior to this matching those on the glabella. In addition, there are prominent spines on the posterolateral cranial corners; the anterior border, however (Pl. 15, fig. 16b) is without spines; the palpebral lobe is inconspicuous at cephalic mid-length.

Librigena has a prominent, and somewhat elevated eye lobe; on the genal field there are two spines; the lateral border is well defined, rounded, and carries only two or three comparatively subdued spines at its mid part; a thoracic segment can be confidently associated because it shows paired axial spines, and also two pleural spines, the inner one at the point of downward geniculation of the segment; the tips of the spines appear to be perforated.



DISCUSSION. The morphology of *Dimeropyge? ericina* is very unusual, and in fact has no direct comparison among mature or nearly mature material of any other dimeropygid. It may be understood, however, by reference to the very early developmental morphology of *Dimeropyge*. It is well established that the protaspis protocranium of members of this genus, as well as cranidia probably assignable to meraspis degree 0 or 1, have only two pairs of glabellar spines and four pairs of fixigenal tubercles (Tripp & Evitt 1983: pl. 31, figs 6, 7, 10, 11, 16, 17, 23, pl. 32, fig. 6; Chatterton 1994: figs 4.3, 4.6, 4.8, 4.22, 4.23, 5.1). These tubercles are in identical positions to the cranial spines of *D.? ericina*. In addition, early (M3) meraspis transitory pygidia of *Dimeropyge* show unreleased thoracic segments with paired axial and fulcral spines similar in position to those seen in a thoracic segment of the Irish species (compare Chatterton 1994: fig. 4.4 with Pl. 16, fig. 19). Finally, *D.? ericina* has a fine, transverse row of rounded tubercles aligned along the rear of its anterior border (Pl. 16, fig. 18) identical to that seen in juvenile *Dimeropyge* (e.g., Chatterton 1994: figs 4.9, 5.1, 6.2). From this it may be hypothesized that *D.? ericina* is a paedomorph, derived through neoteny from an earlier dimeropygid. Much more information would be required, both on the morphology of the Tourmakeady species and on relevant contemporaneous and earlier diversity, to form an opinion about the close affinity of the species. Its lack of genal spines, for example, indicates it may not be derived from ingroup *Dimeropyge*, which as far as is known maintains elongate genal spines from the earliest ontogenetic stages. For this reason, we have assigned it only provisionally to the genus.

Family **SCHARYIIDAE** Osmólska, 1957

Genus **PROSCHARYIA** Peng, 1990

TYPE SPECIES. *Proscharyia sinensis* Peng, 1990, Madaoyu Formation (Upper Tremadoc), northwest Hunan, south China; by original designation.

DISCUSSION. *Protarchaegonus sanduensis* Zhou, 1981, from the lower Tremadoc Guotang Formation, Guizhou, is very similar to the type species and definitely belongs to *Proscharyia*.

***Proscharyia platylimbata* sp. nov.**

Pl. 15, figs ?3, ?4; Pl. 16, figs 7–10, 12–16

ETYMOLOGY. Greek *platys*, broad, and Latin *limbatus*, bordered.

DIAGNOSIS. *Proscharyia* having eyes distant from glabella and preocular sutures divergent at low angle; glabella tapers forward gently and glabellar furrows effaced; prelabellar field comparatively short (sag.); pygidial axis gently tapering.

HOLOTYPE. Cranidium, It. 26161 (Pl. 16, fig. 9); paratypes It. 26118, 26159, 26160, 26162–26167; questionably assigned specimens It. 26142, 26143.

DISCUSSION. Peng (1990) gave a full description of the type species, *Proscharyia sinensis*, which is very like the new species in most features. Only points of difference require discussion here. The glabella of the type species tapers more strongly forwards (the closest specimen is that figured by Peng 1990: pl. 19, fig. 8) and the glabellar furrows are more strongly incised. On the Irish specimens only the posterior glabellar furrow is visible, whereas two or three pairs are seen on the Chinese species; however, the latter are known from internal moulds, on which glabellar furrows are usually clearer. The palpebral lobes of the Tourmakeady species are further from the glabella, such that the width of the interocular cheek is well over half that of the adjacent glabella (tr.), while it is under half in the Chinese species. The divergence of the anterior branches of the facial sutures is concomitantly less, and on some specimens (Pl. 16, fig. 8) they hardly diverge at all. However, on *P. platylimbata* the prelabellar field is much shorter (sag.) relative to the length of the anterior border. On *P. sinensis* the length of the prelabellar field exceeds that of the border as measured along the sagittal line, whereas on *P. platylimbata* the border is the longer. Pygidia of *P. platylimbata* are very similar to those of *P. sinensis* and both are unusual among post-Cambrian trilobites in having well-defined segments which extend all the way to the pygidial margin. The better definition of the pleural and interpleural furrows on the Chinese species is probably a consequence of the internal mold preservation on which the species was based.

Family **RAYMONDINIDAE** Clark, 1924

Glaphuridae Hupé, 1953.

DISCUSSION. As outlined by Ludvigsen and Westrop (*in* Ludvigsen *et al.*, 1989: 61), Lochman-Balk's (*in* Moore, 1959) *Treatise* classification of Raymondinidae included ten Marjuman genera together with the late Sunwaptan *Raymondina*. Palmer (1962) and Rasetti (1965) transferred most of these taxa to Cedariidae, and Ludvigsen and Westrop considered the family Raymondinidae to be monotypic. As such, it contained only three species, known only from cranial (in one case cephalic) material. Ludvigsen and Westrop's illustrations, however, reveal essential correspondence in most cephalic features between *Raymondina* and the Ordovician *Glaphurus*.

Most striking is the shared modification of the basal glabellar area, in which S1 is isolated from the axial furrow and aligned exsagittally, L1 and L2 are merged, and L2 is gently swollen. A second prominent similarity is the occurrence in either taxon of medially yolked librigenae. This was established for *Glaphurus* by

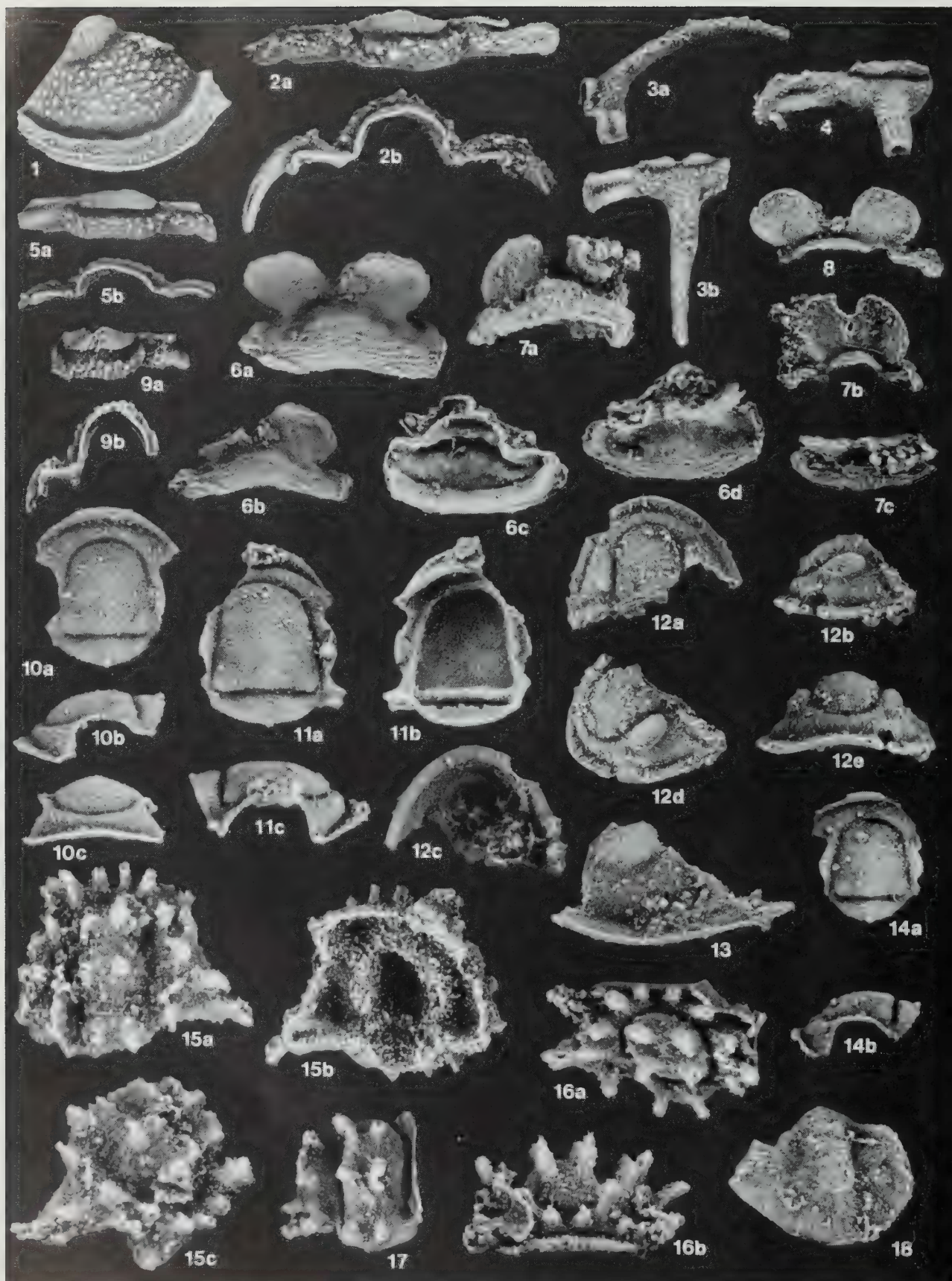
PLATE 14

Figs 1–17 *Celmus michaelmus* sp. nov. **1a–c**, It. 12853, cranidium, dorsal, left lateral, and anterior views, $\times 10$ (figured Fortey & Owens 1975: fig. 1A). **2a–d**, It. 26120, cranidium, dorsal, ventral, left lateral, and anterior views, $\times 10$. **3**, It. 26121, cranidium, dorsal view, $\times 10$. **4a–c**, It. 26123, **holotype**, cranidium, dorsal, ventral, and right lateral views, $\times 10$. **5a–b**, It. 26122, cranidium, dorsal and left lateral views, $\times 10$. **6a–c**, It. 26124, cranidium, dorsal, anterior, and right lateral views, $\times 7.5$. **7a–b**, It. 26125, cranidium, dorsal and right lateral views, $\times 7.5$. **8a–b**, It. 26126, cranidium, left lateral and dorsal views, $\times 10$. **9a–b**, It. 26127, cranidium, left lateral and dorsal views, $\times 10$. **10**, It. 26128, right librigena, external view, $\times 10$. **11**, It. 26129, left librigena, external view, $\times 10$. **12**, It. 26130, left librigena, external view, $\times 10$. **13**, It. 26131, left librigena, external view, $\times 10$. **14**, It. 26132, left librigena, external view, $\times 10$. **15**, It. 26133, left librigena, external view, $\times 10$. **16**, It. 26134, left librigena, external view, $\times 10$. **17**, It. 26135, right librigena, internal view, $\times 10$, view, $\times 15$.

Figs 6, 7, 9, 10 *Phaseolops ceryx* sp. nov. **6**, It. 12856, cranidium, dorsal view, $\times 15$. **7a–b**, It. 12857, cranidium, dorsal and left lateral views, $\times 15$. **9**, It. 26116, cranidium, dorsal view, $\times 15$; **10**, It. 26117, cranidium, dorsal view, $\times 15$.

Fig. 8 *Proscharyia platylimbata* sp. nov. It. 26118, pygidium, dorsal view, $\times 15$.

Fig. 11 *Glaphurus crinitus* sp. nov. It. 26119, cranidium, dorsal view, $\times 10$.



Whittington (1963: 52, pl. 8, fig. 14) and is confirmed by the Tourmakeady material (Pl. 17, fig. 1c, 1e). The same condition in *Raymondina immarginata* has been illustrated by Ludvigsen and Westrop (in Ludvigsen *et al.*, 1989, pl. 50, figs 13, 14). Finally, the genera are almost identical in overall cephalic/cranial dimensions and distribution of features (e.g., forward eye position, median occipital node on anterior edge of L0). There is every reason to consider these shared character-states synapomorphic, and the genera closely related.

As a consequence, separation at the familial level is artificial. Retention of Glaphuridae would result in taxonomic pseudoextinction of Raymondinidae across the Cambrian-Ordovician boundary. Hence, Glaphuridae is placed in subjective junior synonymy of Raymondinidae, which is recognized as a clade with a stratigraphic range from uppermost Cambrian to Upper Ordovician.

Genus *GLAPHURUS* Raymond, 1905

TYPE SPECIES. *Arionellus pustulatus* Walcott, 1877, Lower Ordovician, New York State; by original designation (see Shaw 1968 for complete documentation of the species).

OTHER SPECIES. *Glaphurus alimbeticus* Balashova, 1961, Tremadoc, Kazakhstan; *G. coronatus* Maksimova in Nikiforova, 1955, Tremadoc (Uskud Stage), Siberia; *G. divisus* Whittington, 1963, Whitehornian, western Newfoundland; *G. latior* Ulrich, 1930, Alabama and Virginia; *Glaphurus* sp. of Ross (1972: 31).

Glaphurus crinitus sp. nov. Pl. 17, figs 1–17

1975 *Glaphurus* sp., Fortey & Owens : 230, fig. 1C.

ETYMOLOGY. Latin for hairy.

DIAGNOSIS. *Glaphurus* with densely tuberculate exoskeletal surface and tubercles of two sizes; glabella subrectangular; S2 not pit-like.

HOLOTYPE. Cephalon, It 26177 (Pl. 17, fig. 1); paratypes It 12855, 26119, 26178–26192.

DESCRIPTION. Cranidium trapezoidal in outline, with maximum width at posterior border, being 1.5–1.6 times the sagittal length (excluding anterior spines) in dorsal view in mature cranidia, and somewhat less in immature ones; entire silicified cephalon shows broad anterior arch (Pl. 17, fig. 1c) and that the free cheeks in life position were steeply declined, with the genal spines directed outwards; glabella occupies three-quarters cranial length, and less than half its width, its outline rounded-subrectangular, widest at midlength circumscribed by deep furrows; S0 is of similar depth; L0 with median tubercle positioned immediately behind the furrow;

glabellar furrows emphasized as smooth patches of the exoskeleton; S1 shows a deepened, exsagittally aligned inner portion, whereas the shallow outer part runs approximately transversely towards the axial furrow; the deepened part amounts to 20% of glabellar length; S2 is short, slightly backward-directed; the short eyes are positioned anterior to S2, and the transverse distance between them is twice that of the intervening glabella; preglabellar field with length (sag., as seen in dorsal view) similar to that of L0, downslowing and bulging-convex; deep cranial border furrow; the anterior border carries long, stout, anteriorly splayed spines; no border is perfectly preserved, but the bases of four such spines are seen separated by shorter spines; the anterior cranial margin lies beneath these spines.

Librigenae without connective sutures along narrow doublure, which apparently lacks terrace lines; facial suture cuts posterior border very close to genal spine (Pl. 17, fig. 13), and runs inwards-forwards from there, arching outwards gently at middle of postocular section; at the genal angle there is a very deep pit in the doublure (Pl. 17, fig. 11b); eye elevated on a socle, which is deeper anteriorly; the structure of the lateral border is complex: dorsally it carries an array of alternating stout and small spines like those on the cranial border; beneath this there is another row of tiny spines which run all the way around the cephalic margin and finish under the genal spine (Pl. 17, figs 1c, 15b); below this again, at the edge of the doublure, there is a minutely scalloped edge (Pl. 17, figs 11b, 15b); genal spine short and stout, carrying many smaller spines.

Sculpture of densely packed tubercles of two sizes; a thoracic segment (Pl. 17, fig. 16) carries similar tubercles on the axis and posterior part of the pleurae; it resembles the anterior segment of *G. pustulatus*, as figured by Shaw (1968, pl. 8, fig. 9).

Small cranidia (Pl. 17, figs 8–10) have narrower glabellae than larger ones, and posterior glabellar furrow is of more usual form, curving inwards and backwards; the smallest cranidium (Pl. 17, fig. 10) has a median occipital spine.

Hypostome and pygidium unknown.

DISCUSSION. This stratigraphically early *Glaphurus* species retains several plesiomorphic characters: the glabella is subrectangular, while the anterior glabellar furrow is not pit-like, and the posterior furrow shorter (exsag.) than is the case in the type species, *G. pustulatus*, which has a rounded glabella. The Tremadocian species *G. alimbeticus* Balashova, 1961, from Kazakhstan, has an even more transverse anterior glabellar margin. The sculpture on this species, and on *G. pustulatus*, is much coarser than on the Irish species. The closest species is probably *G. divisus* Whittington, 1963, from western Newfoundland, which, however, has a rounded glabella like the type species, and lacks the anterior cephalic arch of *G. crinitus*. Whittington (1963: pl. 9, fig. 3) also illustrated three pairs of conspicuously large tubercles on the pre-occipital glabella which are more prominent than their counterparts in *G. crinitus*.

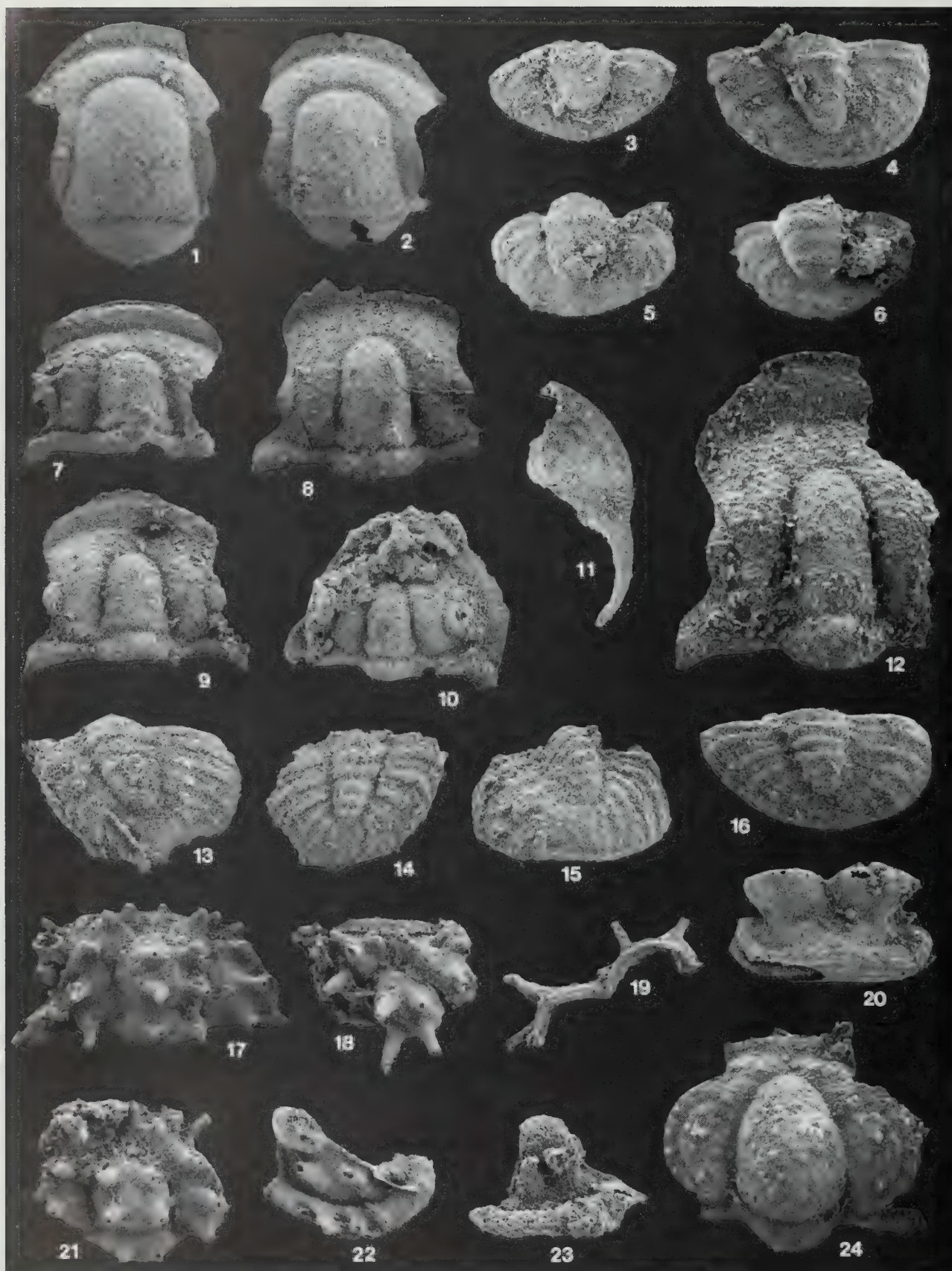
PLATE 15

Figs 1, 2, 5–9 *Celmus michaelmus* sp. nov. **1**, It. 26136, left librigena, external view, $\times 7.5$. **2a–b**, It. 26137, thoracic segment, dorsal and anterior views, $\times 10$. **5a–b**, It. 26138, thoracic segment, dorsal and anterior views, $\times 10$. **6a–d**, It. 26139, pygidium (specimen broken slightly during photography), posterodorsal, posterior, ventral, and dorsal views, $\times 12$ and $\times 10$. **7a–c**, It. 26140, pygidium, posterior, anterior, and dorsal views, $\times 12$, $\times 10$, $\times 10$. **8**, It. 12854, pygidium, anterior view, $\times 10$ (figured Fortey & Owens 1975: fig. 1B). **9a–b**, It. 26141, thoracic segment, dorsal and anterior views, $\times 10$.

Figs 3, 4 *Proscharyia platylimbata* sp. nov. **3a–b**, It. 26142, thoracic segment, left lateral and dorsal views, $\times 15$. **4**, It. 26143, thoracic segment, dorsal view, $\times 15$.

Figs 10–14, 18 *Phaseolops ceryx* sp. nov. **10a–c**, It. 26144, cranidium, dorsal, left lateral, and anterior views, $\times 15$. **11a–c**, It. 26145, **holotype**, cranidium, dorsal, ventral, and right lateral views, $\times 15$. **12a–e**, It. 26146, cephalon, dorsal, left lateral, ventral, oblique, and anterior views, $\times 10$. **13**, It. 26147, left librigena, external view, $\times 15$. **14a–b**, It. 26148, cranidium, dorsal and left lateral views, $\times 15$. **18**, It. 26149, pygidium, dorsal view, $\times 15$.

Figs 15–17 *Dimeropyge? ericina* sp. nov. **15a–c**, It. 26150, **holotype**, cranidium, dorsal, ventral, and oblique views, $\times 15$. **16a–b**, It. 26151, cranidium, dorsal and anterior views, $\times 15$. **17**, It. 26152, cranidium, dorsal view, $\times 15$.



Family **TROPIDOCORYPHIDAE** Pribyl, 1946Genus **PHASEOLOPS** Whittington, 1963

TYPE SPECIES. *Phaseolops sepositus* Whittington, 1963, from the Cow Head Group (Whiterockian), western Newfoundland, Canada; by monotypy.

DISCUSSION. Whittington (1963) described *Phaseolops sepositus* as the oldest known proetid species, assigning it to the subfamily Phacopidellinae Hupé, 1953 (now generally regarded as a synonym of Tropidocoryphinae Pribyl, 1946). Hu subsequently (1971) erected *P. conus*, a species based upon mis-associated aulacopleurid cranidia and tropidocoryphid librigenae and pygidia (see Adrain & Chatterton 1995: 310). The taxon is not related to *P. sepositus*, but rather is an aulacopleurid, and will be revised in a forthcoming work by J.M.A. The only species subsequently assigned to the genus are *P. krafti* Šnajdr, 1983, and *Proetus? primulus* Barrande, 1872 (see Šnajdr 1983), from the Czech Republic. Neither is adequately known, but it is possible that they belong here.

Owens (1973a: 80, text-fig. 11) considered *Phaseolops ceryx* to represent the oldest and most primitive known proetid, and derived *P. sepositus* from it with question. He subsequently (in Owens & Hammann 1990) transferred *P. sepositus* to the aulacopleuroidean family Rorringtoniidae. For reasons given below, we consider *P. ceryx* and *P. sepositus* to be closely related, and to represent the base of the radiation of at least the tropidocoryphid proetoids.

Phaseolops ceryx differs from the Newfoundland type species in several obvious respects, but all seem related to effacement. *Phaseolops ceryx* is more similar to younger tropidocoryphids in the lack of prominent tuberculate sculpture and the expression of the glabellar furrows mainly as shallow, smooth depressions on the exoskeleton. *Phaseolops sepositus* differs from virtually all younger taxa in the possession of deep, slot-like glabellar furrows and a robust tuberculate sculpture on the preglabellar area and librigenal field. The species, however, are almost identical in relative cephalic proportions. Particularly striking is the abrupt lateral deflection of the anterior section of the facial suture, so that it is held almost vertically when the cranium is oriented with the palpebral lobe horizontal (Pl. 15, figs 10b, 11c; cf. Whittington 1963: pl. 5, figs 2, 5). Also compelling is the size and position of the median occipital tubercle. In most subsequent tropidocoryphids, this structure is set at more or less half the sagittal length of the occipital ring. In both *P. ceryx* (Pl. 15, figs 10a, 11a, 14a) and *P. sepositus* (Whittington 1963: pl. 5, fig. 4), it is set directly at the posterior margin, and actually protrudes backward from the margin. We regard these conspicuous shared features as synapomorphic, and consider the species, which are essentially contemporaneous, to be congeneric.

Beyond the conventional proetoid morphology of *P. ceryx*, possibly a key indicator of the affinities of *Phaseolops* lies in the thoracic structure of *P. sepositus*. Early tropidocoryphids possess thoracic

pleural tips in which the pleural furrow shallows abruptly adaxial to the tip, and the tip itself is produced laterally as a small, sinuous, posterolaterally directed spine. The morphology is perhaps best observed in *Stenoblepharum* (e.g., *S. warburgae* (Pribyl, 1946), see Owens 1973b, fig. 9C), but is present also in species presently assigned to *Decoroproetus* (e.g., *D. asellus* (Esmark, 1833), see Owens 1973b, fig. 4F) and species of *Ascetopeltis* (e.g., *A. bockeliei* Owens, 1973b, fig. 2A). Exactly the same morphology is seen in *P. sepositus* (Whittington 1963: pl. 5, fig. 1), but not in *Rorringtonia*, which has pointed but not spinose pleural tips (Owens 1981: pl. 1, fig. a). In addition, *P. sepositus* has the general proetoidean thoracic segment number of 10, in agreement with all tropidocoryphids, but in contrast to the 9 segments seen in *Rorringtonia*. For these reasons, *Phaseolops* is herein regarded as a tropidocoryphid.

The genus may prove to be of significance in determining the affinities of Proetoidea. The sister taxon of the group is at present entirely obscure. If the proposed relationship between *Phaseolops ceryx* and *P. sepositus* is correct, it is conceivable that the tuberculate morphology of the latter, with glabellar furrows deeply incised, is a clue to the nature of the sister taxon. Effaced, 'generalized' trilobites are not unknown in the Ibexian. They are generally assigned to the 'hystricurines,' a group which is at present little more than a polyphyletic catchall, and none described thus far share convincing apomorphies with the proetoids. The reason for this may be that following from the morphology of *P. sepositus*, the Lower Ordovician or Upper Cambrian precursor to the group was a non-effaced, tuberculate taxon. Such taxa, including most of the 'hystricurines,' are common in the Sunwaptan and Ibexian. Support for this scenario lies in the sporadic retention of at least tuberculate librigenae in otherwise advanced Ordovician tropidocoryphids (e.g., *Decoroproetus bodai* Owens, 1973b: fig. 4K).

***Phaseolops ceryx* sp. nov.**

Pl. 13, figs 6, 7, 9, 10; Pl. 15, figs 10–14, 18; Pl. 16, figs 1–6

1973a 'Tourmakeady cranium', Owens: 80, text-fig. 11.

1975 *Decoroproetus?* sp., Fortey & Owens: 229, fig. 1d–1f.

ETYMOLOGY. From the Greek noun *keryx*, a herald.

DIAGNOSIS. Glabellar furrows very shallow, nearly effaced; eye socle simple and librigenal field lacking sculpture.

HOLOTYPE. It. 26145 (Pl. 15, fig. 11); paratypes It. 12856, 12857, 26116, 26117, 26144, 26146–26149, 26153–26158.

DESCRIPTION. Cranium with width across midlength of palpebral lobes approx. 75% of length (sag.); glabella and L0 occupying 75–77% of sagittal length of cranium; glabella with maximum width across posterior, approx. equal to length (excluding L0); anterior

PLATE 16

Figs 1–6 *Phaseolops ceryx* sp. nov. **1**, It. 26153, cranium, dorsal view, $\times 27$. **2**, It. 26154, cranium, dorsal view, $\times 33$. **3**, It. 26155, pygidium, dorsal view, $\times 27$. **4**, It. 26156, transitory pygidium, dorsal view, $\times 40$. **5**, It. 26157, pygidium, dorsal view, $\times 27$. **6**, It. 26158, pygidium, dorsal view, $\times 27$.

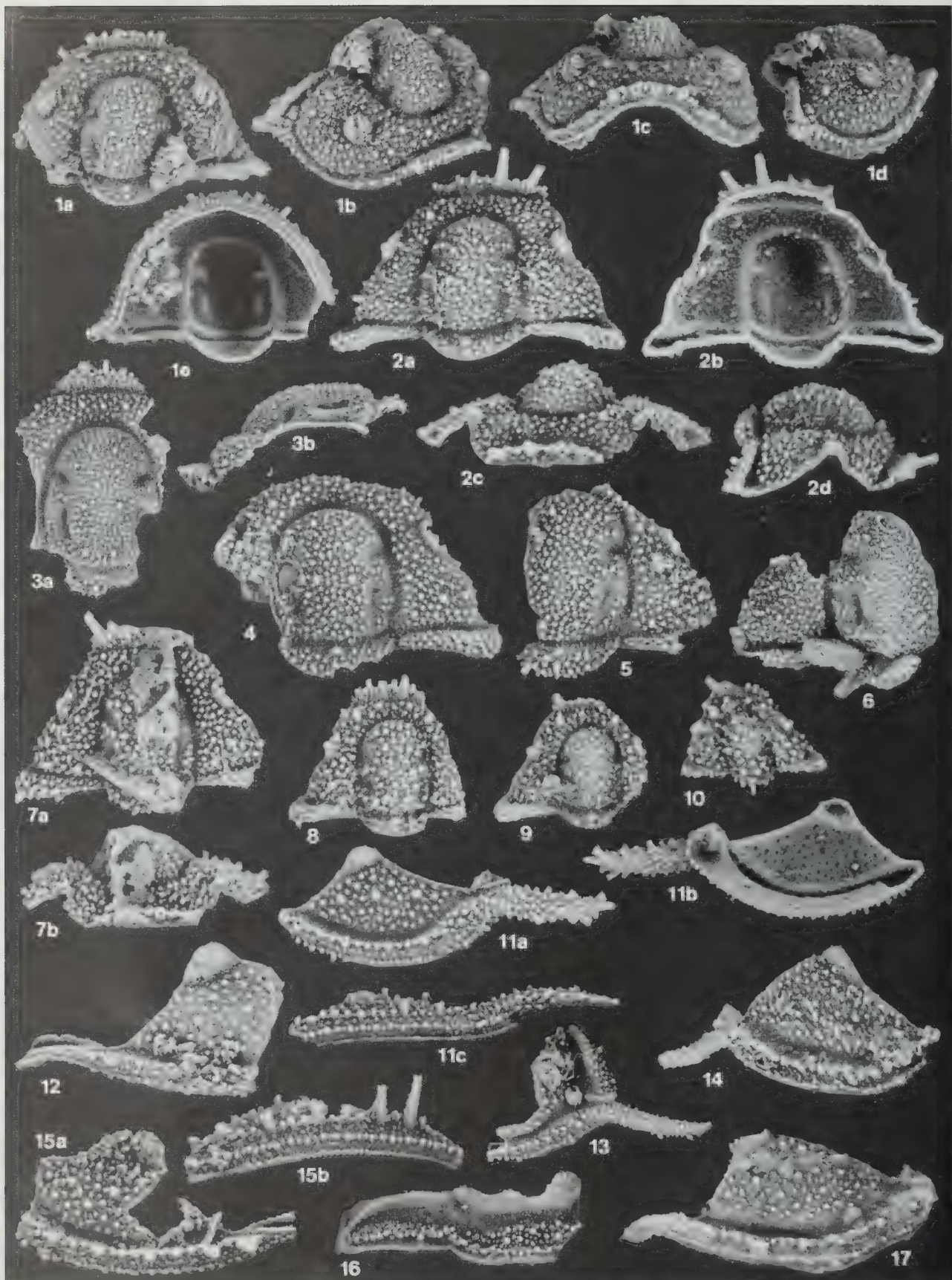
Figs 7–10, 12–16 *Proscharyia platylimbata* 7, It. 26159, cranium, dorsal view, $\times 33$. **8**, It. 26160, cranium, dorsal view, $\times 33$. **9**, It. 26161, **holotype**, cranium, dorsal view, $\times 33$. **10**, It. 26162, cephalon, dorsal view, $\times 27$. **12**, It. 26163, cranium, dorsal view, $\times 60$. **13**, It. 26164, pygidium, dorsal view, $\times 27$. **14**, It. 26165, pygidium, dorsal view, $\times 33$. **15**, It. 26166, pygidium, dorsal view, $\times 40$. **16**, It. 26167, pygidium, dorsal view, $\times 33$.

Figs 11, 20 *Celmus michaelmus* sp. nov. **11**, It. 26168, right librigena, external view, $\times 27$. **20**, It. 26169, pygidium, posterodorsal view, $\times 33$.

Figs 17–19, 21–23 *Dimeropyge? ericina* sp. nov. **17**, It. 26170, cranium, dorsal view, $\times 23$. **18**, It. 26171, cranium, dorsal view, $\times 33$. **19**, It. 26172, thoracic segment, anterior view, $\times 27$. **21**, It. 26173, cranium, dorsal view, $\times 27$. **22**, It. 26174, left librigena, external view, $\times 27$. **23**, It. 26175, left librigena, external view, $\times 33$.

Fig. 24 *Oopsites hibernicus* (Reed in Gardiner & Reynolds, 1909) It. 26176, cranium, dorsal view, $\times 40$.

All figures are scanning electron micrographs.



sections of facial suture with sharp anterior divergence in front of palpebral lobes; cranium moderately vaulted, anterior section of facial suture running subparallel to rear of L0 in lateral profile; cephalic border of continuous even width; cranial anterior border longer medially than laterally due to oblique course of connective sutures; anterior border with considerable dorsal convexity, length (sag.) about two thirds L0, sculpture smooth; anterior border furrow short (sag., exsag.), posterior slope vertical and incised, anterior part with gentler slope leading onto border; preglabellar field slightly longer (sag.) than anterior border, with gentle dorsal convexity and smooth sculpture; axial furrows moderately convergent anteriorly, bowed out slightly around L1, running without interruption into anteriorly convex preglabellar furrow; axial and preglabellar furrows deeply incised, preglabellar furrow with very slight lengthening (sag.) medially; interocular fixigena reduced to narrow, smooth, slope from palpebral lobe to axial furrow; palpebral furrow absent; palpebral lobe elongate but very narrow, lacking obvious sculpture; posterior fixigena reduced to small, narrow triangle; glabella subtrapezoidal, with smooth dorsal sculpture; glabellar furrows very shallow but discernible; L1 with slight independent inflation; S1 relatively elongate (exsag.) and directed posteromedially in distal part, bifurcate proximally, posterior branch nearly reaching S0; S2 originating laterally opposite the anterior third of the palpebral lobe, much shorter than L1, directed posteromedially, not running proximally as far as S1; S3 similar in shape to S2, originating opposite the anterior section of the facial suture in front of the palpebral lobe, anteromedially directed; S0 slightly longer (sag., exsag.) than preglabellar furrow, deep, not as incised as axial furrows, slightly longer behind L1; L0 elongate and shelflike, longest medially, with smooth dorsal sculpture; median occipital node small, protruded posteriorly from posterior margin; axial furrow shallowed greatly opposite L0; posterior border furrow relatively shallow; posterior border short (exsag.), dorsally convex; occipital doublure underlying three quarters the length of L0; fossula not obvious.

Librigenal field with width at midlength of eye 35–40% of exsagittal length, sculpture smooth; eye socle not evident; eye large, width about 60% of exsagittal length; lateral border furrow and posterior border furrow of similar moderate depth; lateral border furrow shallowing abruptly in front of base of genal spine; lateral border not inflated, low dorsal convexity, with single terrace line set laterally and running subparallel to margin; genal spine relatively short and subtriangular, tapering distally to sharp tip; doublure with four or five linear, parallel, and evenly spaced terrace lines.

Rostral plate small and subtriangular, librigenal terrace lines continuous, with slight offset across connective sutures.

Hypostome and thorax unknown.

Pygidium with sagittal length 62–68% of anterior width; axis 68–69% of sagittal length of pygidium; three axial rings present, becoming increasingly less well defined posteriorly; first ring furrow well impressed, second very shallow; axial furrows gently convergent, forming broad arc posteriorly to completely define rear of axis; three pleural and two interpleural furrows defined, posteriormost almost completely effaced; furrows stop short of pygidial margin, but no true border developed.

DISCUSSION. *Phaseolops ceryx* is distinguished from *P. sepositus* in the effacement of its glabellar furrows, lack of tuberculate sculpture on preglabellar and librigenal fields, lack of eye socle, and possession of pygidium with a smooth versus broken margin.

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PLATE 17

Figs 1–17 *Glaphurus crinitus* sp. nov. **1a–e**, It. 26177, holotype, cephalon, dorsal, oblique, anterior, right lateral, and ventral views, $\times 10$. **2a–d**, It. 26178, cranium, dorsal, ventral, anterior, and right lateral views, $\times 15$. **3a–b**, It. 26179, cranium, dorsal and left lateral views, $\times 15$. **4**, It. 26180, cranium, dorsal view, $\times 15$. **5**, It. 26181, cranium, dorsal view, $\times 10$. **6**, It. 26182, cranium, dorsal view, $\times 10$. **7a–b**, It. 26183, cranium, dorsal and anterior views, $\times 15$. **8**, It. 26184, cranium, dorsal view, $\times 15$. **9**, It. 12855, cranium, dorsal view, $\times 15$ (figured Fortey & Owens 1975: fig. 1C). **10**, It. 26185, cranium, dorsal view, $\times 15$. **11a–c**, It. 26186, left librigena, external, internal, and ventrolateral views, $\times 15$. **12**, It. 26187, left librigena, external view, $\times 15$. **13**, It. 26189, cranial fragment and left librigena, external view, $\times 10$. **14**, It. 26190, right librigena, external view, $\times 10$. **15a–b**, It. 26188, right librigena, external and ventrolateral views, $\times 15$. **16**, It. 26191, thoracic segment, dorsal view, $\times 10$. **17**, It. 26192, left librigena, external view, $\times 10$.

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